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AN INQUIRY INTO THE NATURAL CLASSIFICATION OF THE DRYOPOIDEA, BASED PARTLY ON A STUDY OF THEIR INTERNAL ANATOMY (COL.)

By H. E. Hinton, Ph.D.

(*Junior Curator, University Museum of Zoology, Cambridge.*)

With One Plate and One Hundred and Five Text-figures.

(Read 1st March, 1939.)

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Introduction.

IN this paper the relationships of a number of families and genera formerly associated with or referred to the family DRYOPIDAE are discussed. In every case my opinion differs widely from those previously held regarding the position of these groups in a phylogenetic classification. The reason for this divergence of opinion seems to me to be that whereas previous workers have confined themselves either solely to characters of the external anatomy of the adults or, as Böving, and Böving and Craighead, have recently done, solely to characters of the external anatomy of the larvae, I have tried to use both external and internal characters of all stages before coming to a conclusion.

Tradition has exerted a paralysing grip on many fields of science, but nowhere is this more evident than in systematic entomology. The choice of the characters which are used to-day in analysing the degrees of relationship in classifications which purport to be genuinely phylogenetic appears to be governed largely, if not entirely, by the ease with which they may be examined. Thus it is, that in the classifications of the various groups, particularly those of sub-ordinal rank, it is the rare exception and not the rule to find any mention whatever of internal characters. It is my belief that no genuinely scientific system can be evolved on the basis of an arbitrarily selected set of readily available external characters.

For each section of this paper there is a summary in the form of a key which lists the differences between the particular groups under discussion. And it is in these summaries that the reader may see for himself how much light is shed by a consideration of the internal anatomy on the problem of building a natural classification.

Acknowledgments.

My best thanks are due to Dr. A. D. Imms, F.R.S., and Dr. W. H. Thorpe for their advice and criticism during the course of this work. I am particularly

indebted to Dr. G. Salt for reading carefully the manuscript and offering numerous suggestions which have increased such value as this paper may have. I am also grateful to Dr. H. Scott for determining two LIMNICHIDAE.

Method.

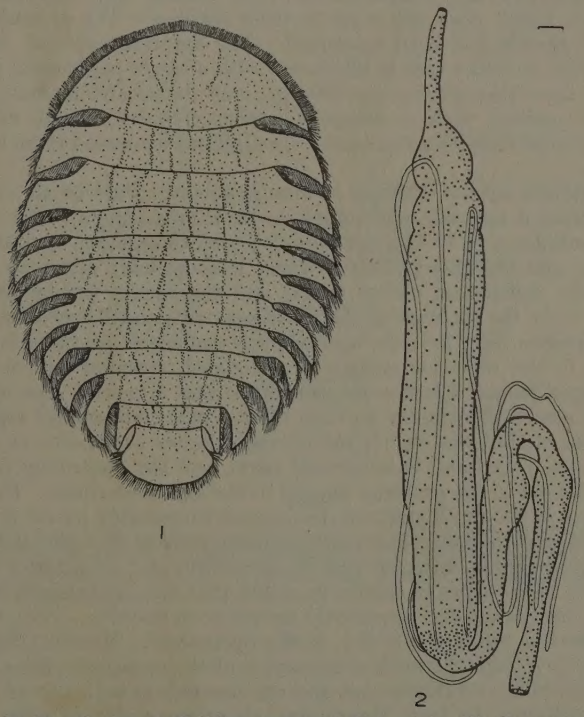
All drawings were made by myself with the aid of a camera lucida. Lines next to figures correspond to a length of 0·20 mm. unless otherwise indicated.

A comparison between the DRYOPIDAE and ELMIDAE.

Larvae.

1. *External anatomy.*

The larvae of the DRYOPIDAE are usually aquatic, but a few, e.g. some *Dryops*, are terrestrial. They vary from being parallel-sided and cylindrical to being onisciform and rather flat (fig. 1). In the parallel-sided forms the head is



FIGS. 1–2.—(1) Dorsal view of *Helichus musgravei* Hntn. (?); (2) alimentary canal of an Indian species of *Helichus*.

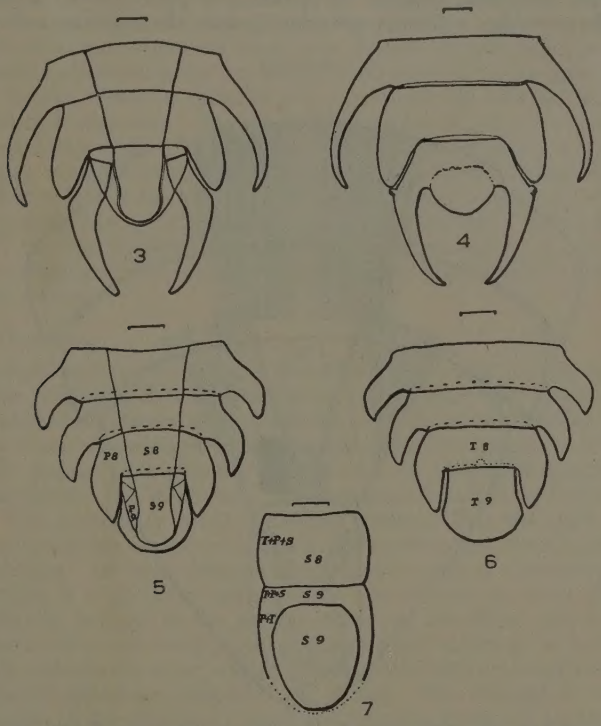
always exposed from a dorsal view, while in the oval forms the head is completely concealed from above by the pronotum. The head is oval or rectangular, and on its dorsal surface is always a short coronal suture which gives rise anteriorly to frontal sutures which diverge forwards and extend to the anterior

margin on each side near the base of the antenna. On each side of the head there may be one pigment spot or ocellus or as many as six. The antennae are 3-segmented. The clypeus and labrum are distinct. The mandibles of most have apical teeth, though a few species are known to have no teeth, and a prostheca may be present or absent. The maxilla never has a distinct articulating area, the stipes apparently never has a palpifer, the galea and lacinia are separate, and the palp is always 4-segmented (Pruthi, 1929, has figured a 3-segmented palp for an Indian species of *Helichus*, but I have been unable to verify this and believe he has overlooked the fourth segment which is very small in many species of *Helichus*). Böving (1926) claims in error that the maxillary palp of all DRYOPIDAE is 3-segmented. The prementum always has a 2-segmented palp and frequently also a palpiger. The postmentum is invariably undivided. Böving (1929) and Böving and Craighead (1931) have figured a species of *Helichus* with the postmentum divided into a large mentum and a large submentum. Closely related species have been examined and found to have the postmentum undivided. It may be mentioned here that in both the ELMIDAE and PSEPHENIDAE these authors have figured a divided postmentum which does not occur in these families. The musculature of a number of species has been examined. The submento-mental muscles are always absent, as is the case in all insects with a single postmental plate (Das, 1937). In some DRYOPIDAE, e.g. *Dryops*, only dorsal and median premental muscles are present, while in others, e.g. some *Helichus*, dorsal, median, and lateral premental muscles are present. In all forms examined there is a distinct gula plate.

The abdomen always consists of nine segments. Part or all of the ninth sternum forms a movable operculum in all known genera. The operculum has been considered to be the sternum of the tenth segment by Böving (1929) and Böving and Craighead (1931). These authors have given no reasons to support their conclusion. West (1929) and the earlier writers consider the operculum to be the sternum of the ninth segment, and I concur in this view. In some *Helichus* (figs. 3–6) the operculum is connected by the intersegmental membrane to the posterior margin of the eighth sternum and on each side well-developed pleural sclerites are present, so that a ventral view of the ninth segment is essentially similar to that of any other abdominal segment. In other species of *Helichus* (fig. 7) the pleural sclerites are absent or completely fused with the tergal and basal sternal parts, and the operculum is no longer directly attached to the posterior margin of the eighth sternum. In this latter case the base of the ninth sternum has become immovably joined to the tergopleural parts and the hinge has migrated posteriorly so that the ninth sternum consists of a posterior movable part or operculum and an anterior fixed part. And in both these types it should be noted that the lateral retractors of the operculum are similar and apparently homologous muscles. Both types have median retractor muscles inserted on the operculum. Hinton (1936 : 76) has shown that in *Dryops* the median retractors of the operculum arise on the anterior margin of the ninth segment and are inserted on each side of the middle of the operculum. In most DRYOPIDAE there are a pair of opercular claws attached to the dorsal membrane of the operculum. These claws are more or less well sclerotised and have a varying number of retractor muscles which arise on the anterior margin of the ninth segment and are inserted in the basal portion of the claw. Among those DRYOPIDAE which have the body onisciform, e.g. some *Helichus*, well-developed claws are absent, and in these cases there are two large and soft subconical lobes which are apparently homologous to the

claws, at any rate judging from the similar musculature. All the segments of the abdomen have discrete pleural sclerites in those larvae which are oval and flattened. The parallel-sided and cylindrical larvae may have, e.g. *Dryops*, no discrete pleural sclerites on the abdomen, and the posterior segments form complete sclerotised rings.

Spiracles may be present on the mesothorax and first eight abdominal segments or they may occur only on the eighth abdominal segment. All spiracles are biforous. Anal retractile gills are generally present but in a few,



FIGS. 3–7.—(3) Ventral view of the three apical abdominal segments of an Indian species of *Helichus*; (4) dorsal view of same; (5) ventral view of the last four abdominal segments of an Indian species of *Helichus*; (6) dorsal view of same; (7) ventral view of the last two abdominal segments of *Helichus substriatus* Mull.

e.g. *Dryops*, gills are completely absent. Böving (1929) and Böving and Craighead (1931) in their classification of the superfamily Dryopoidea use as one of the principal characters the presence or absence of a terminal cloacal chamber. This chamber is the space about the rectum which is occupied by the anal gills and opercular claws when these are retracted. Among members of the same genus, e.g. *Helichus*, gills may be present or absent, and when gills are absent there is no longer about the rectum any space which can be called a chamber.

All known larvae of the ELMIDAE are aquatic, and the mature larvae only leave the water when they are ready to pupate. The body may be rather flat

and onisciform to cylindrical and parallel-sided. In the parallel-sided forms the head is always exposed from a dorsal view, while in those which have an oval body the head is frequently concealed from above by the pronotum. The head is oval or rectangular and is always provided with an epicranial suture which has a relatively short coronal part that divides anteriorly to form the two frontal sutures, each of which extends to the anterior margin. On each side of the head there may be one pigment spot or ocellus or as many as six. The antennae are 3-segmented. The mandible usually has three apical teeth but these are sometimes absent. A prostheca is present in all known forms. The maxilla never has a distinct articulating area, the stipes apparently never

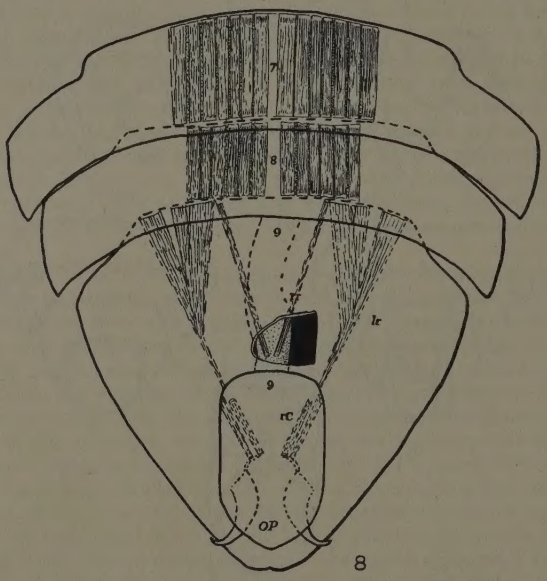


FIG. 8.—Musculature of operculum of *Phanocerus clavicornis* Sharp. (rr) Retractor muscles which are inserted on membrane surrounding rectum. (lr) Lateral retractors of the operculum. (rC) Retractors of claw.

has a palpifer, the galea and lacinia are separate, and the palp is always 4-segmented. Böving (1929) and Böving and Craighead (1931) have figured a 3-segmented palp for *Limnius*, but they have omitted the fourth segment which is rather small. The prementum always has a 2-segmented palp and is occasionally provided with a palpiger. The postmentum is invariably undivided and submento-mental muscles are absent. In several Larini and Elmini examined the dorsal, lateral, and median premental muscles were present. The gula appears to be always well developed.

The abdomen always consists of nine segments, and the posterior part of the ninth sternum always forms a movable operculum, while the anterior part is solidly connected to the pleuro-tergal elements. In the ELMIDAE discrete

pleural sclerites are never present in the ninth segment. The musculature of the operculum (fig. 8) has been investigated for 25 genera of Larini and Elmini and in all found to be the same. Unlike the DRYOPIDAE, there are no median retractors but only lateral retractors similar to those of the DRYOPIDAE. The opercular claws always have two pairs of retractor muscles which have their origin on the anterior sides of the operculum itself and their insertion on the basal part of the claws. I have found the difference between the musculature of the operculum of the DRYOPIDAE and ELMIDAE an absolutely certain way of separating the members of these two families. In all known ELMIDAE the opercular claws are well developed and well sclerotised. In some genera the first eight abdominal segments may have discrete pleural sclerites, while in others discrete pleural sclerites are restricted to a few of the anterior segments.

In all known ELMIDAE spiracles are present on the mesothorax and first eight abdominal segments. Susskind (1935), in her study of the morphology of the respiratory system in *Stenelmis* larvae, has described and figured in detail a pair of metathoracic spiracles and their tracheal connections. Since metathoracic spiracles are unknown among the ELMIDAE and related families and are certainly not present in other species of *Stenelmis* I have been able to examine, I can only conclude that her description and figure are in error. All spiracles are biforous and usually annular. Three tufts of anal retractile gills are always present.

2. *Internal anatomy.*

The central nervous system, the alimentary canal, and the tracheal system of a number of species of both DRYOPIDAE and ELMIDAE have been examined. The central nervous system of both families is similar in all essentials and there are always three thoracic and eight abdominal discrete ganglia. As the form of the body changes from parallel-sided to oval, the abdominal ganglia become more concentrated, but in no case have they been found to be fused with one another. The alimentary canal is likewise similar. The oral part or buccal cavity is not structurally differentiated from the pharynx, which is followed by the oesophagus. In both families the posterior end of the oesophagus or proventriculus is slightly invaginated into the mid-gut to form the cardiac valve. Slightly anterior to the cardiac valve on the dorsal side is a sclerite which I have called the oesophageal sclerite when describing the larvae. Anterior to this sclerite the inner walls of the proventriculus are lined with a broad ring of heavily sclerotised tubercles and spines. The mid-gut is usually the longest section of the alimentary canal and its outer surface is always smooth, *i.e.* there are no projecting regenerative crypts. The hind gut is feebly looped in the parallel forms, but in the onisciform species, e.g. *Helichus* fig. 2, the hind gut has a very long loop. The Malpighian tubules always end freely in the body cavity. Among the DRYOPIDAE they appear to be constantly six, but some ELMIDAE, e.g. *Neoelmis*, have four. The tracheal system is essentially similar in both families, but in the ELMIDAE members of both the Larini and Elmini may have tracheal air sacs. Snodgrass (1935 : 448) says that tracheal air sacs are absent among holometabolous larvae, but they have been known among the ELMIDAE since Dufour's paper of 1862.

Pupae.

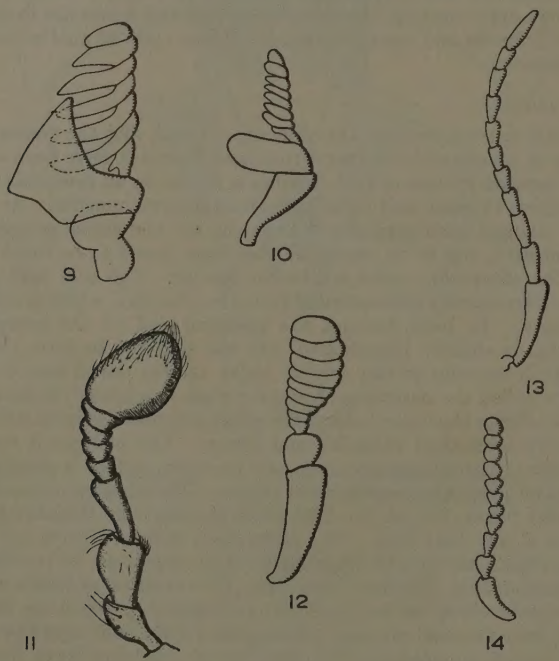
Few pupae of these two families have been described, and my collection contains only a few, so that the generalisations made here may well prove incorrect. In the DRYOPIDAE (*Dryops*) the posterior margin of the second

tergite, the anterior margin of the seventh, and both posterior and anterior margins of the third to sixth are provided with heavily sclerotised transverse bars. In the ELMIDAE (*Potamophilus*, *Hexanchorus*, *Limnius*, *Elmis*, *Riolus*, *Latelmis*, *Dupophilus*, *Macronychus*, *Stenelmis*, *Macrelmis*, and *Elsianus*) there are no heavily sclerotised bars on the abdominal tergites. All known ELMIDAE have at least two large posterior spines on the ninth abdominal segment, whereas in the DRYOPIDAE only one median spine is present here. These are characters of the pupal cuticle. The pupae of the two families can also be distinguished by the form of the adult antenna which is visible through the pupal cuticle. In the DRYOPIDAE the apical segments of the antenna always form a close pectinate club, while in the ELMIDAE they are filiform or clubbed but never form a close pectinate club.

Adults.

1. *External anatomy.*

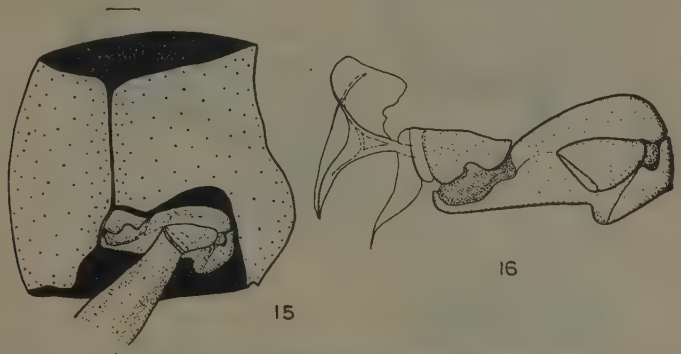
The DRYOPIDAE have the segments of the antenna beyond the second or third always forming a close pectinate club (figs. 9–10), whereas the antenna



FIGS. 9–14.—(9) Antenna of *Dryops* sp. (?); (10) antenna of *Ahaggaria acutangula* Bollow; (11) *Zaitzevia parvula* (Horn); (12) *Dryopomorphus extraneus* Hntn.; (13) *Stenelmoides rufulus* Hntn.; (14) *Stetholus elongatus* C. & Z.

of the ELMIDAE is usually filiform (figs. 13–14), but in a few genera the apical segments form a closely united club (figs. 11–12), though this club is never pectinate.

The structure of the propleural region has been used for about a century to divide the DRYOPIDAE (DRYOPIDAE plus ELMIDAE) into subfamilies and tribes. But before entering into a discussion of the prothoracic pleural region in the DRYOPIDAE and ELMIDAE, it seems necessary to clarify the meaning of the various statements applied to this region in the Coleoptera as a whole. It was first pointed out by Gahan (1910, 1911) and later by Carpentier (1929) and Ferris (1935) that in the suborder Polyphaga there is no notopleural suture, while in the Adephaga this suture is always present. This statement is morphologically incorrect. A notopleural suture is always externally visible in the Adephaga, but one is also externally visible in many groups of the Polyphaga, *e.g.*, DRYOPIDAE, BYRRHIDAE, CANTHARIDAE, etc. In the Polyphaga this is the suture visible between the trochantin and the hypomeron or deflexed part of the notum. In point of fact, it may be said that wherever the trochantin is externally visible in the Polyphaga, such a suture is visible, for the trochantin as defined by Snodgrass (1935) is the precoxal sclerite of a thoracic pleuron derived from the anterior part of the primitive coxopleurite. The significant



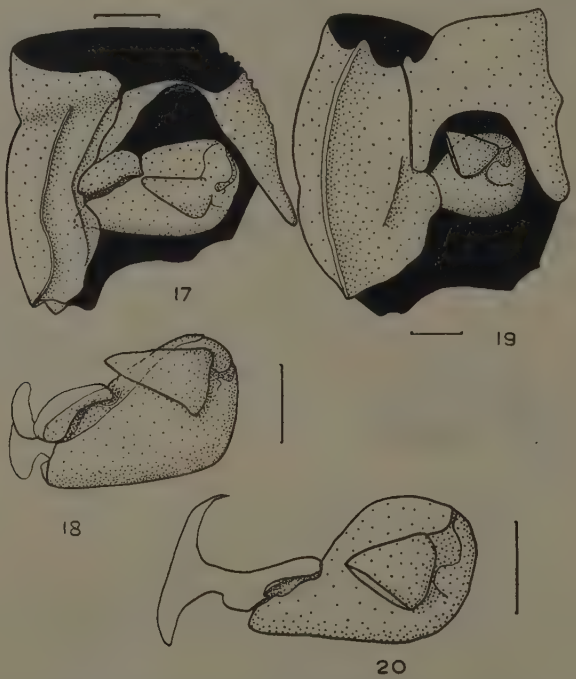
FIGS. 15–16.—(15) Lateral view of prothorax of *Helichus suturalis* Lec.; (16) coxa and trochantin of same dissected out.

difference between the two suborders in this connection lies in the fact that in the Adephaga not only is the pre-articular part of the coxopleurite, the trochantin, present as a separate sclerite which in many forms is externally visible, *e.g.* some CARABIDAE, but also there is another pleural plate representing the fusion of the anapleurite and part of the coxopleurite. This plate resulting from the fusion of the two supracoxal arches is always separated from the hypomeron by the notopleural suture and may be more or less distinctly divided into an anterior piece known as the episternum and a posterior piece known as the epimeron. In the Polyphaga the anapleurite and all of the coxopleurite except the trochantin is lost. The trochantin is often visible externally and often concealed by a projection of the hypomeron or sternum.

In the DRYOPIDAE the trochantin is always present and not as is sometimes stated (*e.g.* Bradley, 1930) absent in certain groups. In most DRYOPIDAE (*Elmomorphus* Sharp is an exception) it is externally visible and associated with transverse front coxae (figs. 15–16). In the ELMIDAE a similar condition prevails among most of the Larini (figs. 17–18). In some of the Larini, e.g. *Phanocerus*, and in many of the Elmini, e.g. *Simsonia* and *Narpus*, the trochantin is visible if the coxae are rotated caudally. However, in most Elmini

the trochantin is concealed even if the coxae are rotated caudally (figs. 19–20). It seems quite clear that the condition of the trochantin, whether concealed or exposed, is at most a generic character and cannot be used, as it has until now in most of the published classifications, for separating categories higher than genera.

Many writers (Lacordaire, 1854; Leconte, 1861–62; Leconte and Horn, 1883; Ganglbauer, 1904; Reitter, 1911, etc.) have used the fact that in a few Larini the prosternum in front of the coxae is very short with a consequent exposure of the ventral surface of the head, as a character of tribal importance



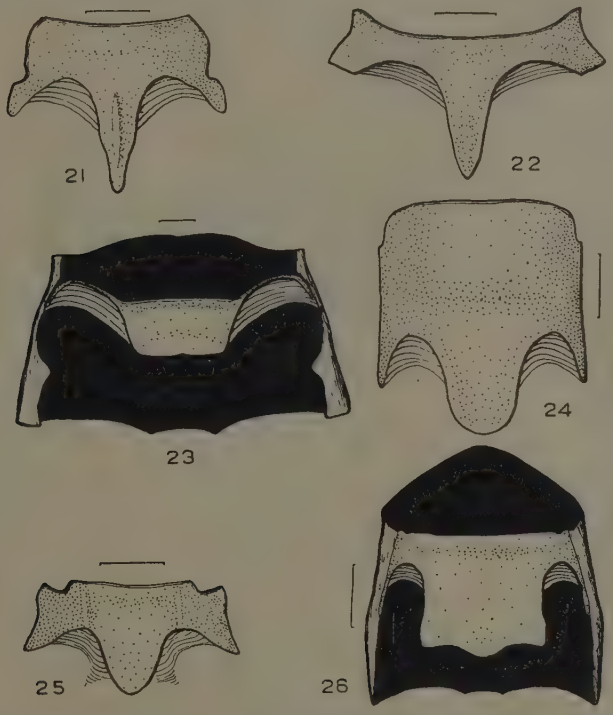
FIGS. 17–20.—(17) Lateral view of prothorax of *Hexanchorus gracilipes* Sharp; (18) coxa and trochantin of same dissected out; (19) lateral view of prothorax of *Cylloepus punctcollis* (Hntn.); (20) coxa and trochantin of same dissected out.

separating the Larini from the DRYOPIDAE. In the forms that have been examined, the degree to which the head appears retracted depends largely upon the length of the prosternum in front of the anterior coxae. In the Larini, the head of *Dryopomorphus* can be retracted so that only the tip of the prementum is exposed from a ventral view. In *Phanocerus* (fig. 21) the head can be retracted up to the base of the prementum, in *Lara* (fig. 22) up to the base of the mentum, and in such forms as *Potamodytes* (fig. 23) and *Hexanchorus* only up to the base of the submentum or the apical portion of the gula. A similar series is found among the Elmini (figs. 24–26) where *Ancyronyx* (fig. 26)

has the prosternum in front of the coxae very short and the head but feebly retractile.

Previous workers have separated the DRYOPIDAE from the Elmini on the structure of the hind coxae which have the posterior face excavated for the reception of the femora. Many of the ELMIDAE, *e.g.* most of the Larini, have the hind coxae as deeply excavated as most of the DRYOPIDAE, so that this character cannot be used to distinguish the DRYOPIDAE from the ELMIDAE.

In all DRYOPIDAE the abdomen has five visible ventral segments, as is also



FIGS. 21–26.—(21) Prosternum of *Phanocerus clavicornis* Sharp; (22) Prosternum of *Lara avara amplipennis* Darl.; (23) same of *Potamodytes antennatus* Dohrn; (24) same of *Stenelmis fuscatus* Blatch.; (25) same of *Ceralimnius corpulentus* (Lec.); (26) same of *Ancyronyx variegatus* (Germ.).

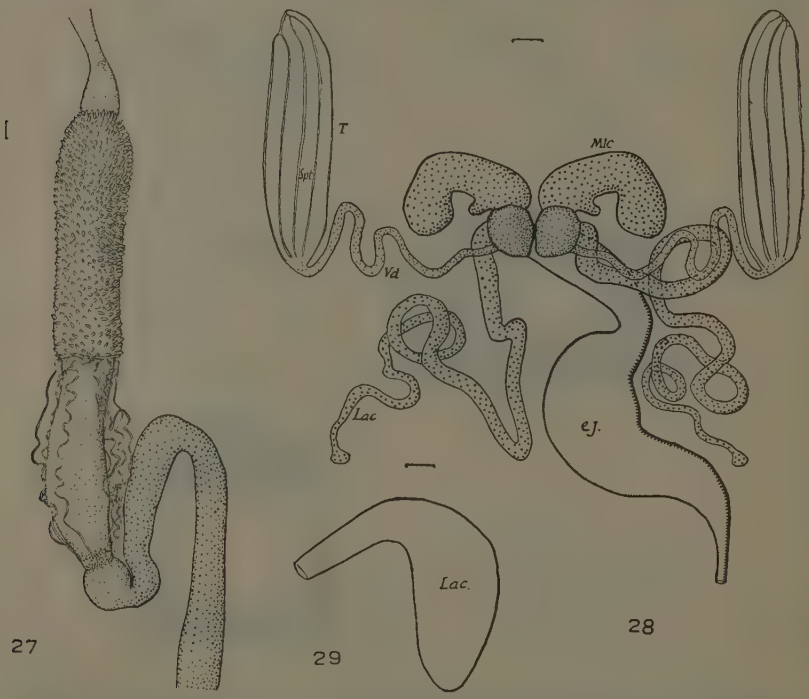
the case in most ELMIDAE. In some Larini, e.g. *Lara*, *Hexanchorus*, *Potamodytes*, etc., there are six visible ventral segments. This number becomes of little significance when it is realised that all that has happened in these Larini is that the sixth, which is ordinarily concealed, is now visible. Some Larini, e.g. *Phanocerus*, have only five visible ventral segments. In both families the number of ventral segments is always six.

The structure of the male genitalia is essentially alike in the two families. The female genitalia of the DRYOPIDAE are nearly always asymmetrical, and styli are never present. Tanner (1927) has described and figured styli in the

female genitalia of *Helichus productus* Lec., but no such structure is present in this or any other species of the genus or family. In the DRYOPIDAE the genitalia generally form a true ovipositor, and the eggs are inserted in plant tissue. The female genitalia of the ELMIDAE are invariably symmetrical and each coxite bears a well-developed movable stylus.

2. *Internal anatomy.*

The alimentary canal of the DRYOPIDAE (fig. 27) has a narrow pharynx followed by the generally broader oesophagus which has the posterior end



FIGS. 27–29.—(27) Alimentary canal of *Helichus bollowi* Hntn.; (28) Male reproductive system of *Helichus bollowi* Hntn.; (29) apex of lateral accessory gland [1] of *H. frater* Hntn. (T) Testes. (Spt.) Sperm tube. (Mlc.) Median accessory gland. (Lac.) Lateral accessory gland. (Vd) Vas deferens. (ej) Ejaculatory duct.

invaginated into the mid-gut to form the cardiac valve. The mid-gut is a straight tube which always has the outer surface densely set with prominent regenerative crypts. There are never any caeca on the anterior margin of the mid-gut. The hind gut of those forms which have been examined is longer than the mid-gut and has a long loop in the region of the abdomen. There are always six Malpighian tubules which do not end freely in the body cavity but are

[1] The gland is always shaped as in fig. 29 and differently from *H. bollowi* Hntn., thus providing a good internal specific character.

embedded in the walls of the hind gut. Dufour (1834) incorrectly described the Malpighian tubules of *Dryops* when he said they ended freely in the body cavity. The male reproductive system (figs. 28–30) has a long ejaculatory duct which opens in the median lobe of the genitalia or is extended beyond it. There is a pair of median accessory glands and a pair of lateral accessory glands. Each testis is composed of six (*Dryops, Helichus*) sperm tubes, each of which is sessile, *i.e.* without a vas efferens and opening directly into the vas deferens. The sperm tubes of each testis are collectively enclosed in a loose, nearly transparent membranous sheath. Dufour (1834) has described and figured the reproductive system of *Dryops auriculatus* Geoffr. His figure and description

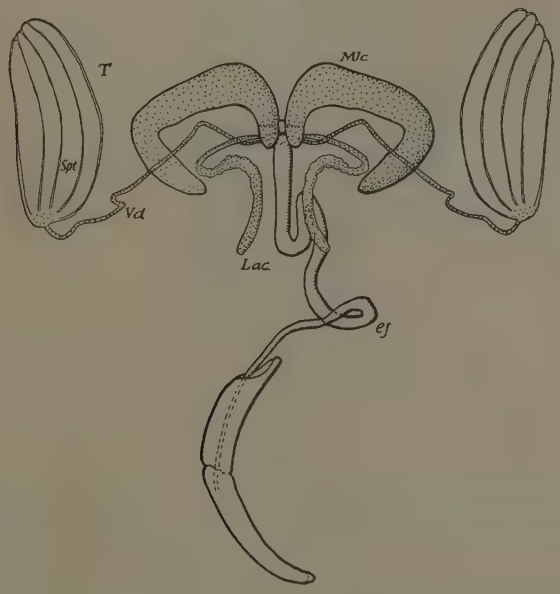


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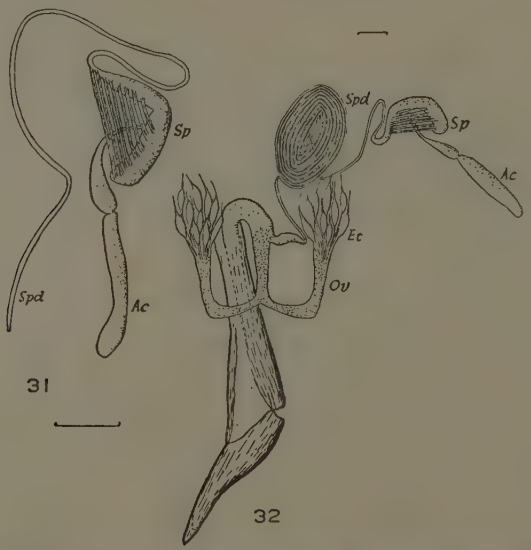
Fig. 30.—Male reproductive system of *Dryops germaini* Grouv. (ej) Ejaculatory duct. (Lac.) Lateral accessory gland. (Mlc) Median accessory gland. (Spt) Sperm tube. (T) Testes. (Vd) Vas deferens.

are very inaccurate. He thought there were only five sperm tubes, whereas six is the correct number for this species, and he failed to notice the thin membranous sheath in which they were enclosed. He believed there was a single pair of accessory glands, but there are two. The female reproductive system (figs. 31–33) has a varying number of egg tubes to each ovary. In *Dryops auriculatus* Geoffr. there are 15 to 20 egg tubes to each ovary, according to Dufour (1834). In *Dryops germaini* Grouv. there are 11 or 12 egg tubes to each ovary. A spermatheca and accessory gland is always present. In some cases the spermathecal duct may be more than twice as long as the entire body, while in others it is only a fraction of the body length. A bursa copulatrix may be present or absent. The central nervous system (figs. 34–36) is as figured.

The alimentary canal of the Elmidae has a narrow pharynx, followed by the generally broader oesophagus which has the posterior end invaginated into the mid-gut to form the cardiac valve. The mid-gut is a straight tube which nearly always has the outer surface smooth, *i.e.* without projecting regenerative crypts, but in one genus, *Elmis* Latr., of twenty genera which have been investigated, the mid-gut has a number of large projecting regenerative crypts. There are frequently no caeca on the anterior margin of the mid-gut, but as many as fourteen may be present here. The hind gut is looped in the region of the abdomen. There are usually six Malpighian tubules, though in *Latelmis* (Dufour, 1835) and in *Neoelmis* there are only four. The distal ends of the Malpighian tubules always end freely in the body cavity, generally near the



Figs. 31–32.—(31) Enlarged view of spermatheca and its accessory gland in *Dryops germaini* Grouv.; (32) female reproductive system of *Dryops germaini*. (Ac) accessory gland. (Et) Egg tubes. (Ov) Oviduct. (Sp) Spermatheca. (Spd) Spermathecal duct.

rectum, and are never embedded in the walls of the hind gut. The male reproductive system has a long ejaculatory duct which opens in the median lobe of the genitalia or beyond. There is a pair of median accessory glands and a pair of lateral accessory glands. Each testis has from one to six sperm tubes, and when there are more than one each sperm tube is pedicellate, *i.e.* it is joined by a distinct vas efferens to the vas deferens. The sperm tubes of each testis are never collectively enclosed in a membranous sheath as is the case among the Dryopidae. The female reproductive system has a varying number of egg tubes to each ovary, the number being two in *Austrolimnius* and about 18 in *Cylloepus*. A spermatheca and an accessory gland is present. All forms so far examined have a bursa copulatrix. The central nervous system is essentially similar to that of the Dryopidae. No differences have yet been

discovered in this system or in the stomodeal nervous system which can be considered to be of family importance.

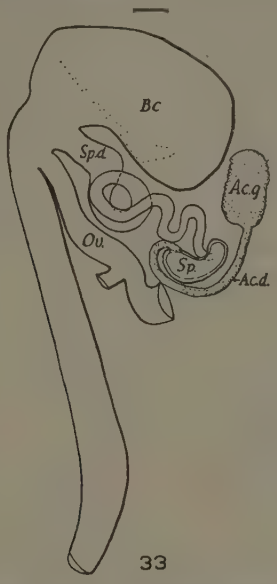


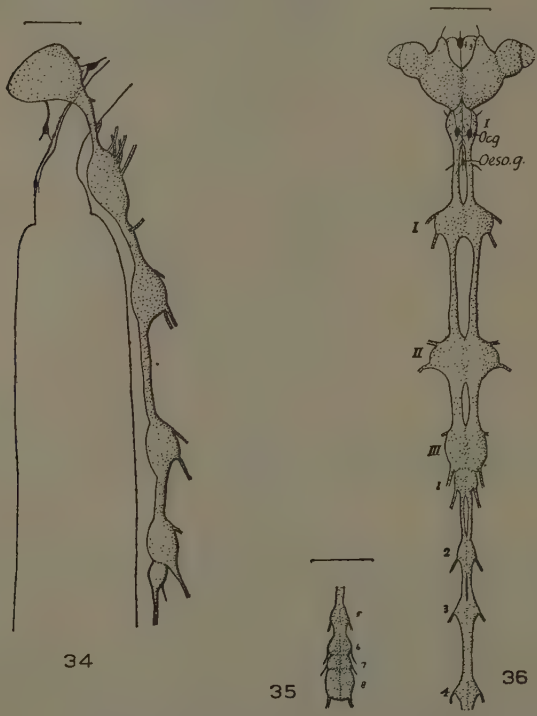
FIG. 33.—Female reproductive system of *Helichus bollowi*. (Ac.d.) Duct of accessory gland. (Ac.g.) Accessory gland. (Bc) Bursa copulatrix. (Ov.) Oviduct. (Sp) Spermatheca. (Sp.d.) Spermathecal duct.

Summary.

The ELMIDAE, formerly considered to be a subfamily of the DRYOPIDAE, are not particularly closely related to the DRYOPIDAE. The ELMIDAE are more distantly related to the DRYOPIDAE than are the LIMNICHIDAE formerly placed in another superfamily. The principal differences between the two families are given in the following key.

1. Adults with the apical segments of the antennae pectinate and forming a close club. Female genitalia without styli and usually asymmetrical. Mid-gut always densely set with projecting regenerative crypts; anterior margin never with caeca. Malpighian tubules always six in number and distal ends always embedded in the walls of the hind gut. Each testis with more than one sperm tube; sperm tubes always sessile and opening directly into the vas deferens, and never with a connecting vas efferens; sperm tubes of each testis collectively enclosed in a membranous sheath. Pupae with abdominal tergites two to seven provided with heavily sclerotised transverse bars. Ninth abdominal segment with a single median spine. Larvae terrestrial or aquatic. Ninth abdominal segment with or without pleural sclerites. Operculum with lateral and median retractor muscles. Opercular claws with the retractor muscles attached to the posterior margin of the ninth segment. Anal retractile gills present or absent. With nine pairs of spiracles or only with the spiracles on the eighth abdominal segment. Tracheae never with air sacs. Malpighian tubules always six in number . . . . . DRYOPIDAE.

–. Adults with the antennae usually filiform, but if clubbed with the segments of the club never pectinate. Female genitalia always with styli and always symmetrical. Mid-gut with the outer surface usually smooth, only rarely set with projecting regenerative crypts; anterior margin usually with caeca but occasionally without. Malpighian tubules usually six but sometimes four in number, and with the distal ends free in the body cavity, never embedded in the walls of the hind gut. Each testis with one or more sperm tubes, and when these are two or more each is pedicellate,



FIGS. 34–36.—(34) Lateral view of central and stomodeal nervous systems of *Helichus bollowi* Hntn.; (35) dorsal view of last four abdominal ganglia of the same species; (36) dorsal view of the central and stomodeal nervous systems of the same species. (Fg) Frontal ganglion. (Ocg) Occipital ganglia. (Oeso.g.) Oesophageal ganglion.

i.e. joined to the vas deferens by a distinct vas efferens: sperm tubes of each side never collectively enclosed in a membranous sheath. Pupae without sclerotised transverse bars on the abdominal tergites. Ninth abdominal segment with two posterior spines. Larvae always aquatic. Ninth abdominal segment never with discrete pleural sclerites. Operculum with only lateral retractor muscles. Opercular claws with the retractor muscles attached to the operculum itself. Anal retractile gills always present. Always with nine pairs of spiracles. Tracheae with or without air sacs. Malpighian tubules usually six though occasionally four in number . . . . . ELMIDAE.

The systematic position of the PELONOMINAE.

PELONOMINAE, Böving and Craighead, 1931, *Ent. Amer.* **11** : 45.

Böving and Craighead (1931) described and figured the larva of *Pelonomus palpalis* Sharp, and to contain the genus *Pelonomus* they erected a new subfamily, the PELONOMINAE. This new subfamily name must be placed in the synonymy of the DRYOPINAE. According to these authors the larva of *Helichus substriatus* Mull. would be placed in the ELMINAE and that of *Helichus lithophilus* Germ. (and related species) in the PELONOMINAE. This latter fact should have been abundantly clear to them from the papers of Erichson (1841), Kellicott (1883), Pruthi (1929), and West (1929). At this time Böving and Craighead suppressed the DRYOPINAE as a synonym of the ELMINAE, part of their confusion being, no doubt, due to the fact that they described and figured as one species parts of two larvae each belonging to a different family. On their plate 71 are five figures of *Dryops auriculatus* Geoffr., and of these figure W is most certainly that of *Dryops*, while figure Z is not and figure V is definitely that of an Elmid, probably *Latelmis* Reitt.

Both larvae and adults of *Pelonomus palpalis* Sharp are very close to those of some sections of the genus *Helichus*, and I do not believe *Pelonomus* can be considered to be more than generically distinct from *Helichus*.

The systematic position of the LARINAE.

Larini, Leconte, 1861–1862, *Classif. Col. N. Amer.* : 116.
Larini, Horn, 1870, *Trans. Amer. ent. Soc.* **3** : 30.
Potamophilaires, Mulsant et Rey, 1872, *Divers* : 11.
Larini, Leconte and Horn, 1883, *Classif. Col. N. Amer.* : 164.
Potamophilini, Kolbe, 1901, *Arch. Naturges.* **1901** (Beiheft) : 136.
Potamophilini, Ganglbauer, 1904, *Kafer Mitteleuropa* **4** (1) : 100.
LARIDAE, Böving, 1929, *Bull. Brooklyn ent. Soc.* **24** : 55.
LARINAE, Böving and Craighead, 1931, *Ent. Amer.* **11** : 45.
LARINAE, Hinton, 1935, *Stylops* **4** : 173.

The genus *Potamophilus* Germar, 1811, the European representative of this group, had always been considered to be a member of the DRYOPINAE, differing from the other genera in having the head free beneath, but Leconte (1861–62) erected the tribe Larini to contain the American *Lara avara*. He placed his new tribe at the beginning of the DRYOPINAE and separated it from the remainder of the subfamily on the following characters (*op. cit.* : 116), " Head not entirely retractile; prosternum not lobed in front; antennae serrate, with the first and second joints not enlarged." This procedure was followed by Horn (1870). Mulsant and Rey (1872) changed the name of the tribe to conform with its oldest genus. This change was adopted by Kolbe (1901 : 136), who unfortunately placed this tribe in the PSEPHENIDAE, apparently untroubled by the enormous difference between the larvae of the two groups. The name Potamophilini was also used by Ganglbauer (1904), Reitter (1911), and most continental authors, but the correct name should be Larini, based on the genus selected as the type by the author of the tribe. Böving (1929) raised the tribe Larini to family rank on the structure of the larva of *Lara*, which he said (*op. cit.* : 67) had an imperfect cloacal chamber, no gills, and six ocelli. Böving and Craighead (1931), realising that Böving's earlier paper was seriously in error as to the structure of the cloacal chamber and the absence of gills, reduced the rank of this group to that of a subfamily which differed from their PELONOMINAE and the ELMINAE in having five ocelli on each side of the head.

I will attempt to show that the LARINAE do not belong to the family DRYOPIDAE but to the ELMIDAE, and that tribal rank for this group is only justified when dealing with the adults.

Larvae.

1. *External anatomy.*

The number of ocelli on each side of the head cannot be used for distinguishing the Larini from the Elmini. All members of the Elmini known to me have a single ocellus on each side, but this is also the case among some genera of the Larini, e.g. *Phanocerus*, while in other genera, e.g. *Hexanchorus*, the various species may have one, five, or six ocelli on each side of the head. Bertrand (1936) considers the Elmini and Larini to be two tribes of the family Dryopidae, and he uses the general body form of *Potamophilus* and the fact that the ninth abdominal segment is forked at the end to separate the Larini from the Elmini. The general body form of *Phanocerus* (Larini) is nearly identical to that of *Phanoceroides* (Elmini), while many Elmini, e.g. *Tolriolus*, have the body form more closely resembling that of *Potamophilus* than do other members of the Larini. In some genera of the Larini, e.g. *Hexanchorus*, the ninth segment may be terminally forked or rounded, while both conditions occur frequently among the Elmini. No character has been found which will separate the whole group Larini (as defined by the adults) from the Elmini. The Larini can be separated from the Elmini only in the way that a purely arbitrary selection of genera from a natural group may be separated from the remainder of genera in that group—that is, by a list of the generic characters.

2. *Internal anatomy.*

The alimentary canal, the tracheal system, and the central nervous system have been investigated in a number of the Larini and Elmini, but no differences have been found which can possibly be considered to be of tribal importance. In each tribe there is a number of genera which possess tracheal air sacs.

Pupae.

Bertrand (1936) has separated the pupae of the Larini from those of the Elmini on the pronotal spines or filaments, which he says are absent among the Larini. The only pupa belonging to the Larini that I have been able to examine (*Hexanchorus*) is essentially similar to those of the Elmini, and, as in many of the Elmini, there is a pair of anterior and a pair of posterior filaments.

Adults.

1. *External anatomy.*

Most of the Larini have the head free beneath. The degree to which the head can be retracted seems to depend largely on the length of the prosternum in front of the anterior coxae. In some Larini (*Phanocerus*, fig. 21) the head can be retracted considerably and the prosternum in front of the anterior coxae is long, while in some Elmini (*Ancyronyx*, fig. 26) the head is as exposed beneath as in most Larini and the prosternum in front of the coxae is very short. In most Larini the front coxae are transverse and the exposed portion of the trochantin is large, while in most Elmini the front coxae are rounded and the trochantin is not externally visible. But in some Larini, e.g. *Phanocerus*, the coxae are feebly transverse and the trochantin of some of the species is only visible if the coxae are rotated caudally, while in some Elmini (*Heterlimnius*, *Simsonia*, etc.) the coxae are feebly transverse and the trochantin is visible if the coxae are rotated caudally. The hind coxae of most Larini have the posterior face deeply excavated to receive the femora, but in some Larini

(*Phanocerus*) this excavation is no deeper than that of most Elmini. In many Larini there are six visible ventral abdominal segments, but in many, e.g. *Phanocerus*, there are only five visible segments. In all Elmini only five ventral segments are visible.

The only character which I have been able to find that can be used to divide the ELMIDAE without exception into two tribes concerns their method of respiration. The Larini are not truly aquatic, but enter the water accidentally or when ovipositing. The entire body is clothed with ordinary hydrofuge hairs, and when they enter the water the whole body is surrounded by a film of air. The Elmini are truly aquatic beetles, seldom or never leaving the water or even coming to the surface. A few individuals of *Elmis maugeti* Latr. were kept by me for over a year in a jar submerged in a tank of water. When these are submerged the entire body is never covered by a film of air, but a film is restricted to certain tracts of fine matted hairs or scales known as tomentum. The usual method of respiration is as follows. While feeding on algae, etc. oxygen bubbles are given off or freed from the intercellular air spaces. These frequently adhere to the portion of the genae near the mouth. The genae are almost always tomentose. By turning the head towards the side of the bubble, the film of air is pushed on to the hypomera or sides of the prosternum. The beetle then pushes the air along to the mesothoracic spiracle or along tracts of tomentum to one of the abdominal spiracles with a patch of tomentum on the anterior face of the front femora; or, when the bubble is as far back as the metathorax, by a similar patch of tomentum on the posterior face of the middle femora. The air is then sucked into the tracheal system. A number of genera have tracts of tomentum on the dorsal surface, and when a bubble of air adheres here it is pushed down to a spiracle by the tomentose apices of the tibiae.

2. *Internal anatomy.*

The alimentary canal, the reproductive system, and the central nervous system have been investigated in a great many species. Two genera of the Larini and about 20 genera of the Elmini have been investigated, and, although excellent generic characters abound, no difference has been found which can be considered to be of tribal importance.

Summary.

In previous classifications the DRYOPIDAE were divided into two subfamilies and of these the DRYOPINAE included the tribes Larini and Dryopini. The Larini were always thought to be more closely related to the Dryopini than to the Elmini. It is here suggested that the Larini are so nearly related to the Elmini that they can only be given tribal rank on a very slight difference in the structure of the adults. In appendix A a new genus of Elmini is described which in every respect, except that of the pubescence, is more closely related to the Larini than to any known genus in its own tribe. A key to the two tribes follows :—

1. Adults terrestrial, rarely entering the water. Body never with tracts of tomentum. Front coxae generally strongly transverse and trochantin exposed. Abdomen frequently with six visible ventral segments Larini.
–. Adults aquatic, seldom or never leaving the water. Body with tracts of tomentum. Front coxae usually round and with the trochantin concealed. Abdomen always with only five visible ventral segments Elmini.

The systematic position of *Lutrochus* Er. and allied genera.

Three genera which are placed to-day in the DRYOPIDAE do not belong here. They are *Lutrochus* Er. referred to the DRYOPIDAE by Erichson (1847), *Ersachus* Er. described in the LIMNICHINAE by Erichson (1847) and removed to the DRYOPIDAE by Sharp (1902), and *Throcinus* Leconte referred by its author (1874) to the DRYOPIDAE. These three genera belong in the LIMNICHIDAE, a family which until now has been considered by most to be no more than a subfamily of the BYRRHIDAE. I try to show that the LIMNICHIDAE do not even belong in the superfamily Byrrhoidea, but when considered from the point of view of the larvae and of the internal and external anatomy of the adults belong to the superfamily Dryopoidea, where they are nearest to the DRYOPIDAE.

LIMNICHIDAE.

Limnichini, Erichson, 1847, *Naturg. Ins. Deutschl.* **3**: 496.
Limnichides, Lacordaire, 1854, *Gen. Col.* **2**: 485.
Limnichites, Jacquelin du Val, 1857–1859, *Gen. Col. d'Eur.* **2**: 267.
LIMNICHIDAE, Thomson, 1860, *Skand. Col.* **2**: 120.
Limnichini, Leconte, 1861–1862, *Classif. Col. N. Amer.*: 112.
Limnichiens, Mulsant et Rey, 1869, *Hist. Nat. Col. Fr.* Piluliform.: 159.
Limnichini, Leconte and Horn, 1883, *Classif. Col. N. Amer.*: 161.
LIMNICHINAE, Sharp, 1902, *Biol. Centr.-Amer. Col.* **2** (1): 673.
Limnichini, Ganglbauer, 1904, *Kaf. Mitteleur.* **4** (1): 52.
LIMNICHINAE, Casey, 1912, *Mem. Col.* **3**: 37

Erichson (1847) erected the tribe Limnichini to contain a few genera of BYRRHIDAE–*Limnichus* Latreille, 1829 and allied genera. Jacquelin du Val (1857–59) also considered the Limnichites to be one of the three groups of the BYRRHIDAE. Thomson (1860) gave the Limnichini family rank and placed it near the DRYOPIDAE (plus ELMIDAE). This arrangement was not followed in the subsequent classifications proposed by Leconte (1861–62), Mulsant and Rey (1869), Leconte and Horn (1883), Ganglbauer (1904), and Casey (1912). All of these authors considered the LIMNICHINAE to be a tribe, or at most a subfamily, of the BYRRHIDAE.

A comparison between the LIMNICHIDAE and BYRRHIDAE.

For the purpose of this study, the BYRRHIDAE are considered to include two subfamilies, BYRRHINAE and AMPHICYRTINAE. Casey (1912) divided the AMPHICYRTINAE into two tribes, the Amphicyrtini and the Lioini. Böving and Craighead (1931) have given subfamily rank to the latter tribe on the basis of larval structure only. Neither adults nor larvae of this group have been available for the present work.

Larvae.

The larvae of both the BYRRHINAE and the AMPHICYRTINAE are well known. For a detailed description of these types see Böving (1929) and Böving and Craighead (1931). The maxilla has a well-developed articulating area. The labium has the postmentum divided into a distinct mentum and submentum. The mandible always has a series of long hairs on the posterior inner margin. There are never any gills, all larvae being terrestrial. There are always ten abdominal segments and the sternite of the ninth is never modified to form an operculum.

The first known Limnichid larva is described in detail in appendix B. Those

characters which are probably of family importance are described here briefly. The mandibles are without a series of long hairs on their inner posterior margins. The postmentum is undivided and submento-mental muscles are absent. The cardo and stipes of the first maxilla are completely fused to the postmental part of the second maxilla, and the maxillary articulating area is absent. The gula is undeveloped. The abdomen has only nine segments and the posterior part of the sternum of the ninth forms a movable operculum which has two strongly sclerotised claws attached to its dorsal membrane. An operculum with lateral and median retractor muscles is present. The opercular claws have the retractor muscles attached to the anterior margin of the ninth segment. The spiracles are annular and biforous and are present on the mesothorax and first eight abdominal segments. The anal tracheal gills are retractile and consist of three tufts.

Adults.

1. *External anatomy.*

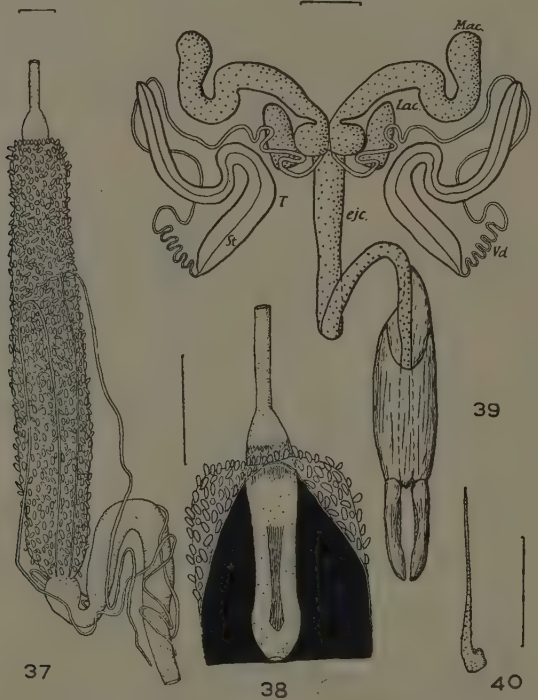
The external differences between the adults of the BYRRHIDAE and LIMNICHIDAE are slight, and when considered by themselves by no means sufficient to place these two families in different superfamilies. In the BYRRHIDAE the clypeus is completely fused to the frons (Ganglbauer, 1904), or if a clypeal suture is present it is obsolete (Casey, 1912). In the LIMNICHIDAE a clypeal suture is always present and the clypeus is large and distinct. The female genitalia of most of the known genera of the BYRRHIDAE have been examined. They are always symmetrical and each coxite is provided with a movable stylus. The female genitalia of the LIMNICHIDAE are symmetrical or asymmetrical, but they are never provided with styli.

2. *Internal anatomy.*

The only published work on the internal anatomy of the BYRRHIDAE is that of Dufour (1834) on the alimentary canal and reproductive system of the female of *Byrrhus pyrenaeus* Duf. The alimentary canal has the mid-gut smooth, *i.e.* without projecting regenerative crypts, and there are no caeca on its anterior margin. There are six Malpighian tubules and the distal ends of these end freely in the body cavity, *i.e.* they are not attached to the walls of the hind gut. The female reproductive system differs in no character that can be considered to be of family importance from that of the LIMNICHIDAE, and is not described here. A single male pupa of *Byrrhus pilula* L. collected in Wiltshire: Mildenhall, viii.1938 (*H. E. Hinton*) was available for the study of the internal structures. The alimentary canal and Malpighian tubules are similar to those of *B. pyrenaeus* Duf. The male reproductive system has to each testis about a dozen sperm tubes which are all pedicellate, each being connected to the vas deferens by a distinct vas efferens. The sperm tubes of each testis are not collectively enclosed in a membranous sheath.

The internal anatomy of five specimens of the subfamily AMPHICYRTINAE, *Amphicyrta* sp.?, has been examined. These were collected in California: Sonora, xii.1930 (*H. E. Hinton*). The alimentary canal has the mid-gut smooth, without projecting regenerative crypts, and without caeca on its anterior margin. There are six Malpighian tubules and the distal ends of these terminate freely in the body cavity, generally near the rectum. The male reproductive system has to each testis apparently five sperm tubes which are distinctly pedicellate, each being connected to the vas deferens by a vas

efferens. The sperm tubes of each testis are not collectively enclosed in a membranous sheath. In all essential characters of the internal anatomy the Byrrhinae and Amphicyrtinae are similar. These two subfamilies are also alike in possessing styli on the coxites of the female genitalia. The details of the external morphology and the structure of the larvae (Böving and Craighead, 1931) all point to the fact that they are closely related groups in the same



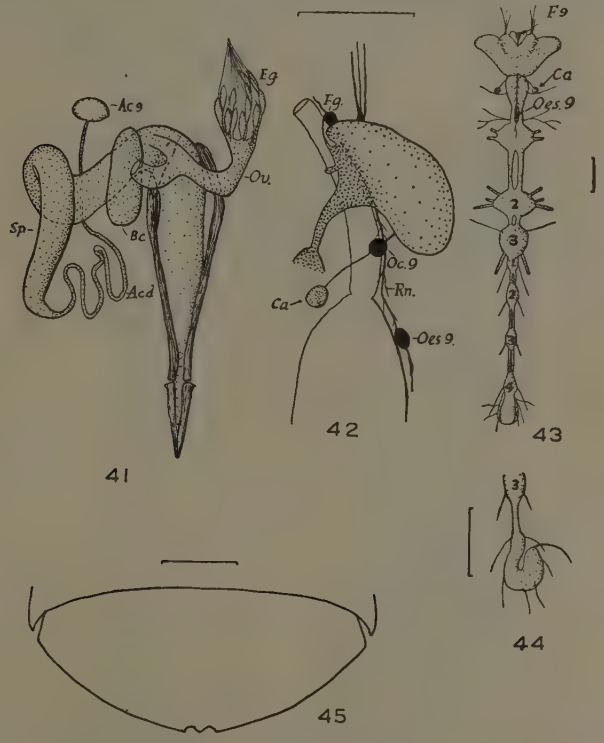
Figs. 37–40.—(37) Alimentary canal of *Byrrhinus* sp.?; (38) anterior portion of mid-gut of same species cut open to show the cardiac valve; (39) male reproductive system of the same species; (40) lateral view of median lobe of male genitalia of the same species. (ejc) Ejaculatory duct. (Lac) Lateral accessory gland. (Mac) Median accessory gland. (St) Sperm tube. (T) Testes. (Vd) Vas deferens.

family. Both subfamilies have similar habits. They are slow-moving beetles, generally found under logs and stones.

The internal anatomy of four genera of the family Limnichidae has been studied in detail, *Byrrhinus* Mots., *Limnichites* Casey, *Ersachus* Er., and *Lutrochus* Er.

A number of specimens of *Byrrhinus* sp. were collected in Brazil: Matto Grosso, Guajara-Mirim, viii.1937 (*H. E. Hinton*). The alimentary canal has the mid-gut densely set with prominent regenerative crypts and there are no caeca on its anterior margin (fig. 37). There are six Malpighian tubules and

the distal ends of these terminate freely near the rectum and are not embedded in the walls of the hind gut. The male reproductive system (fig. 39) has the testis on each side composed of three sperm tubes which are sessile, *i.e.* they open directly into the vas deferens and there is no distinct vas efferens. The sperm tubes of each testis are collectively enclosed in a transparent membranous sheath. The female reproductive system is as figured (fig. 41). The central

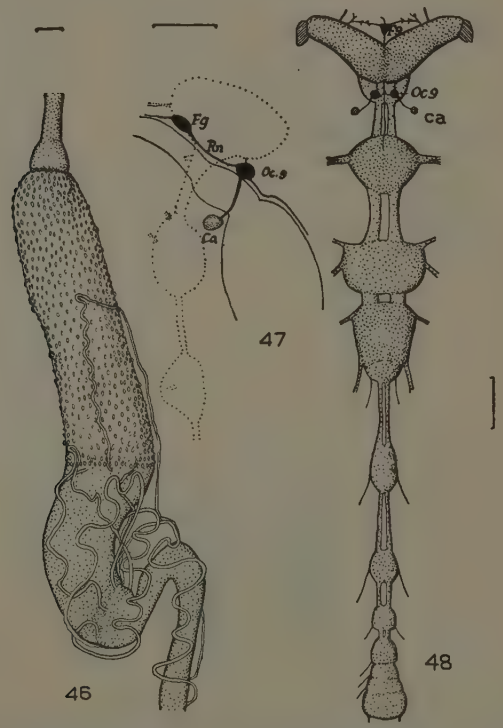


FIGS. 41–45.—(41) Female reproductive system of *Byrrhinus* sp.?; (42) lateral view of brain and stomodeal nervous system of same species; (43) dorsal view of central and stomodeal nervous systems of the same species; (44) lateral view of terminal abdominal ganglion of same species; (45) ventral view of last abdominal segment of female of same species. (Ac.d.) Duct of accessory gland. (Ac.g.) Accessory gland. (Bc) bursa copulatrix. (Ca) Corpora allata. (Eg.) Egg tubes. (Fg) Frontal ganglion. (Oc.g.) Occipital ganglion. (Oes.g.) Oesophageal ganglion. (Ov) Oviduct. (Rn.) recurrent nerve. (Sp) Spermatheca.

nervous system (fig. 43) has three discrete thoracic ganglia; the first abdominal ganglion is fused to the third thoracic, the second and third are free, and the fourth to eighth are fused together, the terminal portion of the last ganglion being bent ventrally and forwards (fig. 44) in all of the dozen or so specimens examined. The stomodeal nervous system (figs. 42 and 43) has a pair of occipital ganglia and a single oesophageal ganglion.

The internal anatomy of two species of the genus *Limnichites* was examined.

one from Brazil: Guajara-Mirim and the other from Bolivia: Yungas Valley, both collected by me (H.E.H.). The mid-gut is densely set with prominent regenerative crypts and there are no caeca on its anterior margin. There are six Malpighian tubules and the distal ends of these end freely in the body cavity. In the male, each testis has six sperm tubes and these are sessile and those of each side are enclosed collectively in a membranous sheath. The female reproductive system and the central nervous system are essentially



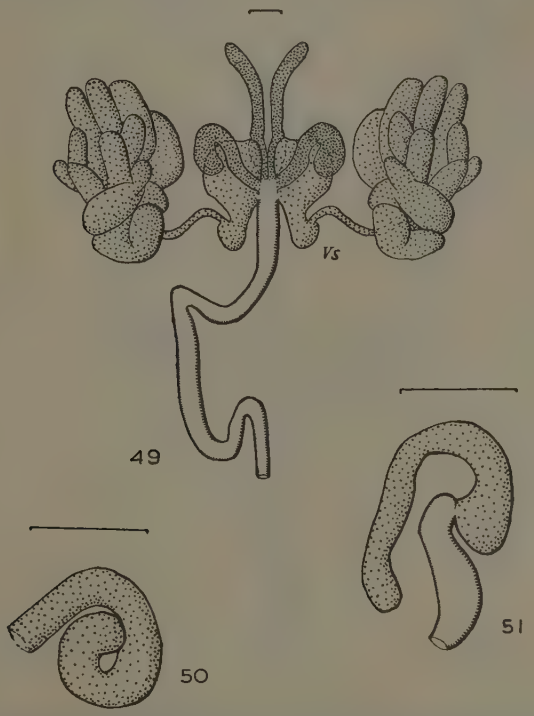
FIGS. 46–48.—*Lutrochus montanus* Grouv. (46) Alimentary canal; (47) lateral view of stomodeal nervous system; (48) dorsal view of central and stomodeal nervous systems. (ca) Corpora allata. (Fg) Frontal ganglion. (Oc.g.) Occipital ganglia. (Rn) Recurrent nerve.

similar to those of *Byrrhinus*, but there are only six instead of twelve egg tubes to each ovary and the last ganglion of the central nervous system is not bent ventrally. The stomodeal nervous system was not examined in this genus.

A small series of males and females of *Ersachus erichsonianus* Sharp have been available for an examination of the internal anatomy. These were collected in Mexico: Dist. de Temascaltepec, Temascaltepec, 1934 (*H. E. Hinton*). The alimentary canal has the mid-gut densely set with prominent regenerative crypts and there are no caeca on its anterior margin. There are

six Malpighian tubules and the distal ends of these terminate freely in the body cavity, generally near the rectum. The male reproductive system has the testis on each side composed of three sperm tubes which are sessile and are collectively enclosed in a membranous sheath. The female reproductive system has a very long spermathecal duct which opens into the apex of the bursa copulatrix and there are about eight egg tubes to each ovary.

One female of *Lutrochus geniculatus* Chev. collected in Cuba: Havana, 7.iii.1937 (*H. E. Hinton*) and one male and two females of *L. montanus* Grouv. collected in Bolivia: Yungas Valley, Chulumani, 9.vi.1937 (*H. E. Hinton*)



FIGS. 49–51.—*Lutrochus montanus* Grouv. (49) Male reproductive system; (50) dorsal view of accessory lateral gland dissected off; (51) left lateral view of right median accessory gland in normal position. In fig. 49 the median accessory glands have been straightened out. (Vs) Vesicula seminalis.

were available for a study of the internal anatomy. The alimentary canal has the mid-gut densely set with prominent regenerative crypts and there are no caeca on its anterior margin (fig. 46). There are six Malpighian tubules and the distal ends of these are embedded in the walls of the hind gut at about the middle of its length. The male reproductive system (fig. 49) has each testis composed of about fourteen (?) sperm tubes which are sessile. No sheath was found over the testes but this may be because the single male was dissected long before I was aware that the testes of some Dryopoidea have the sperm tubes collectively enclosed in a membranous sheath, and the sheath is in any case

often very difficult to find when known to be present. The female reproductive system is as figured (fig. 52), the spermatheca and its accessory gland not being illustrated, as they could not be distinctly seen. The central nervous system (fig. 48) has the three thoracic ganglia discrete, the first abdominal ganglion is fused to the third thoracic, two to four are free, and five to eight are fused together. The stomodeal nervous system has a pair of occipital ganglia and a single oesophageal ganglion.

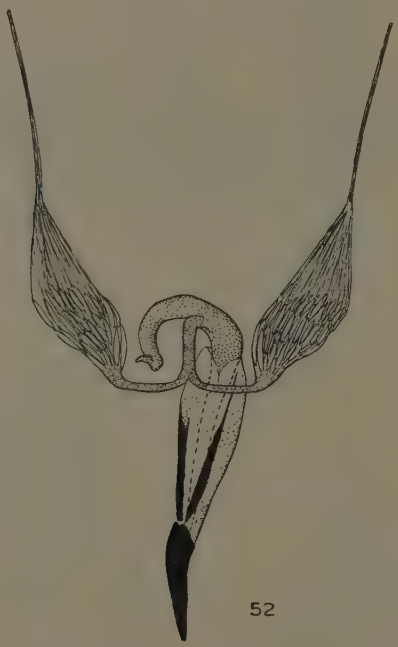


Fig. 52.—Female reproductive system of *Lutrochus montanus* Grouv. If a spermathecal accessory gland is present, it was not seen in the dissection.

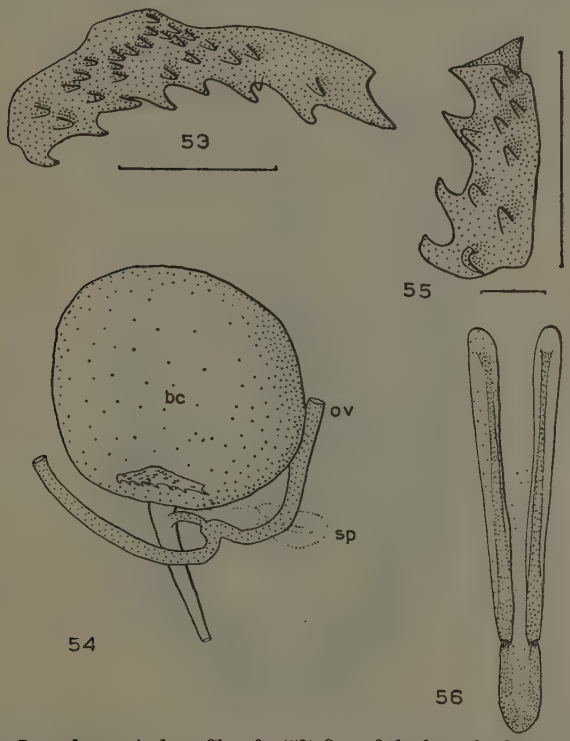
Summary.

The subfamily Limnichinae is given family rank and is transferred from the superfamily Byrrhoidea to the superfamily Dryopoidea. The essential differences between these two families are given in the following key.

1. Adults terrestrial and not associated with water. Without a distinct clypeus. Mid-gut without regenerative crypts. Distal ends of Malpighian tubules free in the body cavity, never embedded in the walls of the hind gut. Testis with the sperm tubes always pedicellate and never collectively enclosed in a sheath. Female genitalia always symmetrical and with a stylus always present on each coxite. Larva terrestrial. Mandible always with a series of long hairs on the inner posterior margin. Maxillary

articulating area well developed. Labium with the postmentum divided into a large mentum and a large submentum. Abdomen of ten segments and ninth sternum never modified to form an operculum. Always without gills . . . . . Byrrhidae.

–. Adults riparian or aquatic, nearly always associated with water. With a large and distinct clypeus. Mid-gut densely set with prominent projecting regenerative crypts. Distal ends of Malpighian tubules free or embedded in the walls of the hind gut. Testes with the sperm tubes of each testis



Figs. 53–56.—*Lutrochus geniculatus* Chev.[2] (53) One of the lateral sclerites of the wall of the bursa copulatrix; (54) female reproductive system. The spermatheca could not be seen distinctly in my only specimen and is probably incorrectly drawn; (55) lateral sclerite of the bursa copulatrix. This one is opposite the one drawn in fig. 53; (56) dorsal view of female genitalia. (bc) bursa copulatrix. (ov) Oviduct. (sp) spermatheca.

always sessile and enclosed collectively in a membranous sheath. Female genitalia symmetrical or asymmetrical but with the coxites never with styli. Larva aquatic or riparian (?). Mandible never hairy on inner posterior margin. Maxilla without an articulating area; stipes and cardo fused to the postmentum which is undivided. Abdomen of only nine segments, and with the ninth sternum modified to form an operculum. Anal tracheal gills present . . . . . Limnichidae.

[2] Note the great differences between this species and *L. montanus* Grouv. These are good internal specific differences.

A comparison between the LIMNICHIDAE and the DRYOPIDAE.

A detailed description of the anatomy of both these families has already been given and will not be repeated here. Only the differences between them will be stressed.

Larvae.

The larvae of the LIMNICHIDAE differ only from those of the DRYOPIDAE in having the stipes and cardo of the maxilla completely fused to the postmental

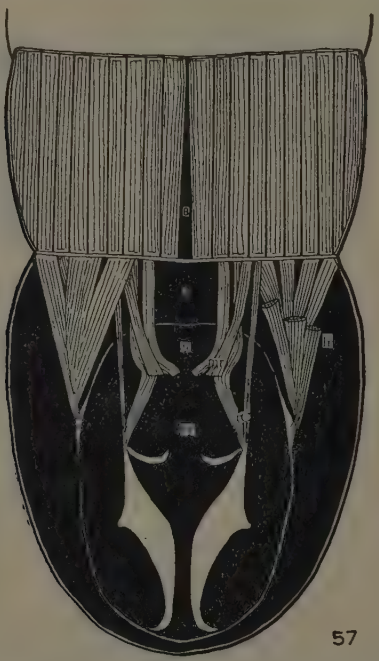


FIG. 57.—Musculature of operculum of larva of *Lutrochus* sp.?. (lr) Lateral retractors of the operculum. (mr) Median retractors of the operculum. (op) Operculum. (rC) Retractors of the claw.

part of the labium, whereas in the DRYOPIDAE the stipes is always separated from the cardo by a well-developed suture and both of these sclerites are separated from the postmentum by distinct sutures. The musculature of the operculum of both families is similar in all essentials. In the LIMNICHIDAE (fig. 57) the operculum has both median and lateral retractor muscles, and the retractors of the claws are attached to the anterior margin of the ninth segment.

Adults.

1. *External anatomy.*

The only difference between the DRYOPIDAE and LIMNICHIDAE I have been able to discover, which applies to all the forms examined, is a difference between

the antennae. In the LIMNICHIDAE the antennae are filiform or with the apical segments forming a club. In the DRYOPIDAE the segments beyond the second or third are always pectinate and form a compact club.

2. *Internal anatomy.*

In most of the LIMNICHIDAE the Malpighian tubules end freely in the body cavity, but in some, e.g. *Lutrochus* Er., the distal ends of the tubules are embedded in the walls of the hind gut. In none of the DRYOPIDAE which have been examined, do the Malpighian tubules end freely in the body cavity, the distal ends being always embedded in the walls of the hind gut.

Summary.

The family LIMNICHIDAE is closer to the DRYOPIDAE than to any other known family when both the external and internal anatomy of the adults and larvae is taken into account—far closer than the ELMIDAE which until now has been considered by most to be a subfamily of the DRYOPIDAE. A key to the two families follows.

1. Adults with the antennae filiform or with the apical segments thickened but never pectinate. Malpighian tubules with the distal ends free in the body cavity, though occasionally embedded in the walls of the hind gut. Larva with the stipes and cardo of the maxilla completely fused to the postmental part of the labium . . . . . LIMNICHIDAE.
–. Adults with the apical segments of the antennae forming a close pectinate club. Malpighian tubules with the distal ends always embedded in the walls of the hind gut. Larva with the stipes and cardo of the maxilla separate and not fused to the postmental part of the labium . DRYOPIDAE.

There are to-day three subfamilies of LIMNICHIDAE : LIMNICHINAE, CEPHALOBYRRHINAE, and THAUMASTODINAE. Nothing is known of the internal anatomy or of the larvae of the last two. The THAUMASTODINAE are in several respects, *e.g.* the obliquely placed hind coxae, the highly modified hind legs, the tarsal formula, and the close approximation of the eyes on the vertex, so different from the other two subfamilies that when the larvae and the internal anatomy of the adults are known they may have to be raised to family rank as suggested by Champion (1924). A key for the separation of these three subfamilies follows

1. Eyes separated on vertex of head by less than the breadth of a single eye. Hind coxae oblique. Tarsal formula 4–5–5 or 4–4–4. Hind tibiae and tarsi with numerous long, stout spines . . . . . THAUMASTODINAE.
–. Eyes separated on vertex by more than the breadth of a single eye. Hind coxae transverse. Tarsal formula always 5–5–5. Hind tibiae and tarsi without long and stout spines . . . . . 2.
2. Hypomera with a transverse or oblique ridge . . . . . LIMNICHINAE.
–. Hypomera without ridges . . . . . CEPHALOBYRRHINAE.

Of the genera placed to-day in the DRYOPIDAE, *Throcinus* Lec. belongs in the CEPHALOBYRRHINAE and *Ersachus* Er. and *Lutrochus* Er. in the LIMNICHINAE. *Ersachus* Er. has a short and poorly developed oblique ridge on the posterior portion of the hypomera, and it seems to represent an intermediate form between the CEPHALOBYRRHINAE and LIMNICHINAE. If the larva and the internal anatomy of the adults prove to be similar to those of the LIMNICHINAE, the two subfamilies will have to be united.

The systematic position of *Psephenoides* Gahan.

The genus *Psephenoides* was described by Gahan (1914) and referred by him to the PSEPHENIDAE, partly on account of the similar habits of the adults and the great general resemblance which the larvae bear to those of *Psephenus*. Champion (1920) when dealing with the adults pointed out that the anterior coxae are strongly transverse and without a visible trochantin, and the abdomen is shining, whereas in *Psephenus* the anterior coxae are globose and have a large exposed trochantin, and the abdomen is scabroso-punctate and opaque. Champion (*op. cit.* : 195) says, " The coxal and abdominal characters remove *Psephenoides* from the Parnid-group PSEPHENINAE as defined by Leconte and Horn, and the genus seems to me to be much more nearly related to the Dascillid-group ATOPINAE and EUBRIINAE, some of the genera of which are doubtless aquatic or subaquatic in their earlier stages." Böving (1926 and 1929) and Böving and Craighead (1931) referred *Psephenoides* to the family DRYOPIDAE. In giving a comparative account of the anatomy of the larvae, pupae, and adults, I try to prove that the genus *Psephenoides* belongs in the family PSEPHENIDAE and is not closely related to the members of the DRYOPIDAE.

A comparison with the family PSEPHENIDAE.

The PSEPHENIDAE are divided into two subfamilies, and for this comparative study I have chosen a genus typical of each.

Larvae.

1. *External anatomy.*

The larva of *Psephenus herricki* De Kay has been described and figured many times. The body is scale-like and the head is completely concealed from a dorsal view by the pronotum. There are six ocelli on each side and the antennae are 3-segmented. The maxilla has a 4-segmented palp and a large and soft articulating area. The labium has the postmentum undivided. The ventral surface of the abdomen has five pairs of large branched gills on segments two to six (West, 1929). Böving (1929 : 59) has said that these gills are on segments one to five, and in the figure given by Böving and Craighead (1931) of this species, the gills are shown on segments one to five. In *Ps. palpalis* Champ., a close relative, the gills are on the posterior border of segments two to six, while in one Indian species before me gills are present on the first six abdominal segments. The ninth abdominal segment has a small but distinct movable operculum and is essentially similar to that of the DRYOPIDAE. Böving and Craighead (1931) claim that a movable operculum is not present in the PSEPHENIDAE, but they can scarcely have examined their specimens of *Psephenus* very closely, for the movable operculum is one of the most conspicuous features of the ninth segment. The other principal difference given by these authors for distinguishing the PSEPHENIDAE from the DRYOPIDAE is the absence of a " cloacal chamber " among the PSEPHENIDAE. By the term " cloacal chamber " they mean the space around the rectum which is occupied by the anal gills when these are retracted. The " cloacal chamber " is a character of very little systematic importance. Among the DRYOPIDAE members of the same genus, e.g. *Helichus*, may or may not have anal gills. Two pairs of spiracles are present : one on the mesothorax and the other on the eighth abdominal segment.

The larva of *Eubrianax* is essentially similar to that of *Psephenus*, but differs principally as follows: (1) the eyes on each side of the head consist of five dorso-lateral faceted ocelli and one large ventro-lateral pigment spot; (2) the maxillary palp is only 2-segmented, as has been pointed out by Blackwelder (1930) and Imms (1933); (3) the eighth abdominal segment is provided with lateral expansions which extend to the margin of the carapace, whereas in *Psephenus* the lateral expansions of this segment are absent; and (4) paired gills are present only on the first four abdominal segments. Böving (1926 and 1929) and Böving and Craighead (1931) either describe or figure the larva of *Eubrianax edwardsi* (Lec.) as having gills on the first five abdominal segments. Blackwelder (1930) in his study of the same species says there are only four pairs of gills, these being on segments two to five. His figure shows four pairs of gills but on segments one to four. I have been able to examine two Indian species and these definitely have the gills on segments one to four.

The larva of *Psephenoides* is similar in general appearance to both *Psephenus* and *Eubrianax*. The head has the antenna 3-segmented and on each side there is a single large pigment spot. The maxilla has a soft and very large articulating area, and the palp is 3-segmented. The labium has the postmentum undivided. There are no ventral gills on the abdomen. The eighth segment is without lateral expansions. The ninth segment is small, the tergite is movable, there are discrete pleural sclerites, and the sternite forms a movable operculum. Three tufts of anal, retractile, tracheal gills are present. According to Böving (1929) rudimentary spiracles are present on the first eight abdominal segments of *Ps. gahani* Champ. In this species there is also a pair of mesothoracic spiracles. In *Ps. immsi* Gahan and *Ps. volatilis* Champ. there are no spiracles.

2. *Internal anatomy.*

The alimentary canal and the central nervous system have been investigated in all three genera and found to be essentially similar. In *Psephenus* and *Psephenoides* the alimentary canal is straight except for one long loop involving the hind gut. In *Eubrianax* the hind gut is relatively shorter and not looped. All three have no caeca on the mid-gut and the outer surface of this organ is smooth. The hind gut has six Malpighian tubules which end freely in the body cavity.

In *Psephenus* the central nervous system has the first two thoracic ganglia widely separated and the third thoracic together with the eight abdominal ganglia forming a closely united mass, though the limits of each ganglion are easily distinguishable. In *Eubrianax* this system is very similar but the third thoracic and the first six abdominal ganglia are not as closely united and may even be called discrete. *Psephenoides* is similar to *Eubrianax* but the seventh and eighth abdominal ganglia are more closely united.

Pupae.

When ready to pupate the mature larva of *Psephenus palpalis* Champ. crawls out of the water to find a suitable place, generally under a stone in a moist place. Pupae and mature larvae have been found as much as 30 to 40 yards from the nearest water, but are usually found under stones or under the moss matting of stones or logs within a few feet of the stream. Pupation occurs beneath the larval skin and the dorsal half of the last instar skin remains loosely attached to the pupa, the ventral half being frequently found still attached to the posterior end of the dorsal half. The pupa is similar to the

pupal type commonly found in the Coleoptera—soft, free, and with the body similar in shape to that of the adult.

Essig (1926) and Blackwelder (1930) have described and figured the pupa of *Eubrianax edwardsi* (Lec.). Pupation takes place under the skin of the last instar larva in the water and the pupae are soldered down to stones under the water. The anterior portion of the dorsal surface of the skin of the last instar larva remains attached to the pupal cuticle, but the posterior portion—segments seven to nine—is lost and its place is occupied by the posterior end of the pupa which is modified to resemble very closely the missing portion of the larval skin.

In *Psephenoides*, as in *Eubrianax*, pupation occurs beneath the surface of the water, but in *Psephenoides* the process begun in *Eubrianax*, of replacing the skin of the last instar larva with a pupal structure which resembles it closely, is completed. The entire dorsal surface of the skin of the pupa of *Psephenoides* is modified so that it bears an extremely close resemblance to the dorsal surface of the larva, and the skin of the last instar larva is completely lost.

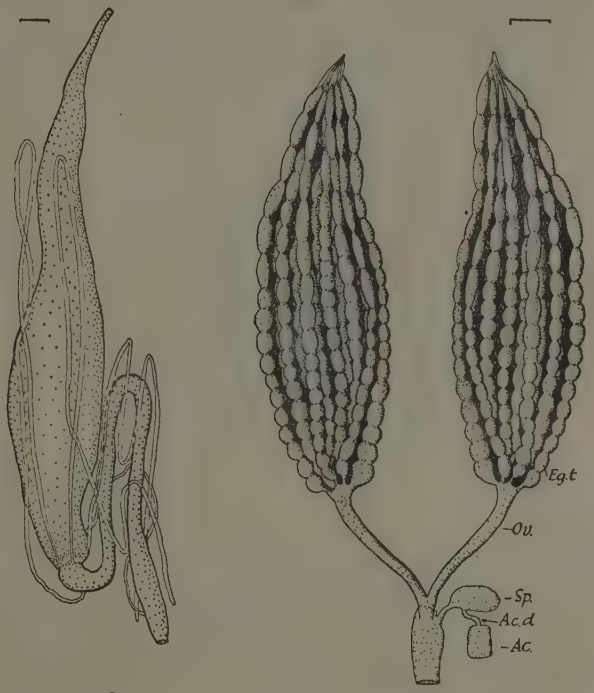
Adults.

1. *External anatomy.*

In all essential details *Psephenoides* is similar to *Psephenus* and *Eubrianax*. The mandibles in all three are weak and small and have only a small and entirely membranous prostheca. In *Psephenus* the postmentum is divided into a large mentum and a large submentum, whereas in *Psephenoides* and *Eubrianax* the postmentum is undivided. In *Psephenus* and *Eubrianax* the scutellum is relatively small, the metanotum is normal, and the elytra meet along the middle line of the body for most of their length. In *Psephenoides* the scutellum is relatively very large, the metanotum is similar to that of the other two genera, and the elytra do not meet along the middle line of the body. Among the species already described there is a considerable amount of variation in the degree to which the elytra approach each other along the middle line of the body. In *Ps. immsi* the elytra are very widely separated but in *Ps. volatilis* they nearly meet, so that great significance cannot be attached to this character as Gahan did (1914 : 188). Of the metanotum of *Ps. immsi*, Gahan (*loc. cit.*) says, " The middle area of the metanotum, behind the broad scutellum, is not grooved along the middle (as in the great majority of beetles), but is convex along the middle and marked with a groove along each side." In a male of *Ps. volatilis* Champ. before me there is a broad groove behind the scutellum as in most beetles and as in *Psephenus* and *Eubrianax*. In a female of *Ps. immsi* and one of *Ps. gahani* the portion which in fresh specimens forms the bottom of the groove has buckled due to drying and now forms the convex portion described by Gahan. It is clear that the convex portion described in such detail by Gahan is nothing more than an artifact. Further proof of this is afforded by the fact that in the pupae of both *Ps. immsi* and *Ps. gahani*, which I have preserved in alcohol, the metanotum is perfectly normal. In *Psephenoides*, contrary to Champion's (1920 : 195) statement, there is a small and slender but distinctly visible trochantin attached to the strongly transverse front coxae. In *Psephenus* the anterior coxae are rounded and the visible portion of the trochantin is very large. The anterior coxae of *Eubrianax*, unlike those of *Psephenus*, are nearly identical in structure to those of *Psephenoides*.

The prosternal process in both *Psephenus* and *Eubrianax* is long and pointed, while in *Psephenoides* it is broadly rounded and short. In transferring

Psephenoides from the PSEPHENIDAE to the DASCILLIDAE Champion's second reason was that the ventral surface of the abdomen in *Psephenus* was scabroso-punctulate and opaque, while that of *Psephenoides* was shining. Some South American forms of the PSEPHENIDAE, e.g. *Pheneps braziliensis* Hntn., have the ventral surface of the abdomen nearly as sparsely punctate and shining as *Psephenoides*, and in any case it does not seem probable that anyone to-day will seriously maintain that a slight difference in the lustre of the abdomen and the density of its punctures is a character of family importance. In *Psephenoides*



FIGS. 58–59.—*Psephenus palpalis* Champ. (58) Alimentary canal; (59) female reproductive system. (Ac) Accessory gland. (Ac.d.) Duct of accessory gland. (Eg.t.) Egg tube. (Ov) Oviduct. (Sp) Spermatheca.

and in all other genera of the PSEPHENIDAE there is a movable stylus on each coxite of the female genitalia.

2. *Internal anatomy.*

The internal anatomy of a female of *Psephenus palpalis* Champ. collected in Mexico has been examined, no other properly preserved specimens being available. The alimentary canal (fig. 58) has the surface of the mid-gut smooth, *i.e.* there are no projecting regenerative crypts. The anterior margin of the mid-gut is without caeca. The hind gut has six Malpighian tubules which end freely in the body cavity. The female reproductive system (fig. 59) has about 30 egg tubes to each ovary. The spermatheca has a short accessory

gland, and the spermathecal duct opens into the apex of the bursa copulatrix. No pupae or adults of *Eubrianax* are available for an examination of the internal anatomy.

The internal anatomy of a female pupa of *Psephenoides volatilis* Champ. has been examined. The alimentary canal has the surface of the mid-gut smooth and the anterior margin of this organ is without caeca. The hind gut has six Malpighian tubules which end freely in the body cavity. The female reproductive system is essentially similar to that of *Psephenus*. The internal anatomy of a male pupa of the same species has been examined. The reproductive system is as figured (fig. 60). Each testis has only one sperm tube which is very similar to the type found in such genera of the ELMIDAE as *Xenelmis* Hntn. A sheath homologous with that which encloses the sperm

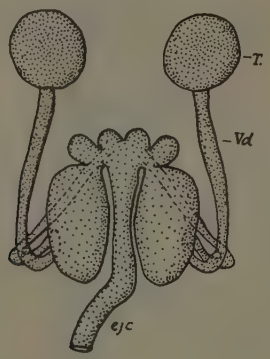


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FIG. 60.—Male reproductive system of *Psephenoides volatilis* Champ. (ejc) Ejaculatory duct. (T) Testes. (Vd) Vas deferens.

tubes when there are more than one in the DRYOPIDAE is here apparently absent.

Summary.

Gahan (1914) referred the genus *Psephenoides* to the PSEPHENIDAE, where I think it is correctly placed. When only the structure of the adults is considered, two alternatives are left. Either this genus is placed in the PSEPHENIDAE or a new family must be erected to contain it. As has been shown above, the differences between *Psephenus* and *Psephenoides* lie chiefly in the structure of the postmentum, elytra, prosternum, and anterior coxae. These differences might easily be considered to be of family importance were it not for the fact that *Eubrianax* has the prosternum and elytra of *Psephenus* and the postmentum and anterior coxae of *Psephenoides*.

If a division of these three genera into two families is to be made on the basis of pupal structure, *Psephenoides* and *Eubrianax* belong to one family and *Psephenus* to another. *Psephenus* has a terrestrial pupa which is normal, but in the other two genera the pupa is aquatic and of a type that deviates

widely from any other known coleopterous pupa. On the other hand, if a division in families is made on the basis of larval structure alone, *Psephenus* and *Eubrianax* would be closely related genera in the same family, while *Psephenoides* might well be considered to be in a family only remotely related to the PSEPHENIDAE.

These considerations should give pause to those who still attempt to build natural systems of classification on the characters of one stage only.

A key to the three subfamilies of PSEPHENIDAE is as follows :—

1. Adults with the postmentum undivided. Anterior coxae strongly transverse and with the externally visible part of the trochantin very small. Pupae aquatic; dorsal surface partly or completely modified to resemble closely the skin of the last instar larva; skin of last instar larva lost or partly attached to the dorsal surface of the pupa . . . . . 2.
–. Adults with the postmentum divided. Anterior coxae more or less rounded and with the externally visible part of the trochantin large. Pupa terrestrial and never modified to resemble the skin of the last instar larva; pupa always concealed beneath skin of last instar larva PSEPHENINAE.
2. Elytra meeting on the middle line of the body. Prosternal process long and pointed. Pupa with the dorsal part of the skin of the last instar larva attached except for the three posterior segments which are replaced by a pupal structure closely resembling them . . . . . EUBRIANACINAE.
–. Elytra not meeting on the middle line of the body. Prosternal process short and broadly rounded. Pupa with the entire dorsal surface modified to resemble closely the skin of the last instar larva; skin of last instar larva entirely lost . . . . . **PSEPHENOIDINAE** subfam. n.

A key to the larvae of the PSEPHENIDAE.

1. Larva with one ocellus on each side. Maxillary palp 3-segmented. Ninth abdominal segment with discrete pleural sclerites. Abdomen without ventral gills but with three tufts of anal retractile gills. With nine pairs of spiracles or without spiracles . . . . . PSEPHENOIDINAE.
–. Larva with more than one ocellus on each side. Maxillary palp 4- or 2-segmented. Ninth abdominal segment without discrete pleural elements. Abdomen with ventral gills but without anal retractile gills. With only two pairs of spiracles . . . . . 2.
2. Larva with six faceted ocelli on each side. Maxillary palp 4-segmented. Eighth abdominal segment without lateral expansions. Abdomen with ventral gills on segments two to six or on segments one to six PSEPHENINAE.
–. Larva with five dorso-lateral faceted ocelli and one ventro-lateral pigment spot. Maxillary palp 2-segmented. Eighth abdominal segment with lateral expansions. Abdomen with ventral gills on segments one to four EUBRIANACINAE.

A comparison between the PSEPHENIDAE and DRYOPIDAE.

Larvae.

1. *External anatomy.*

In all PSEPHENIDAE there is a very large articulating area on the maxilla and this structure is completely absent or extremely small among the DRYOPIDAE. Böving and Craighead (1931) have used this character as their principal one in separating the PSEPHENIDAE and DRYOPIDAE, etc. from the BYRRHIDAE. In his study of *Psephenoides gahani* Böving (1926) has figured and labelled the

maxillary articulating area, and in this respect his figure is based on fact. It is clear that one can no longer use this character to separate the Dryopoidea from the Byrrhoidea. The maxillary palp of all larvae of DRYOPIDAE appears to be 4-segmented (Pruthi, 1929, has figured a 3-segmented palp for an Indian species of *Helichus*, but I have been unable to verify this), while in the PSEPHENIDAE the maxillary palp may be 2-, 3-, or 4-segmented. Böving (1926 : 385) in referring to the maxillary palp says, " . . . no known larvae of the DRYOPIDAE–HELMIDAE have more than a three-jointed palpus." In both these families the maxillary palpus appears to be always 4-segmented. No members of the DRYOPIDAE have ventral abdominal gills as have most of the PSEPHENIDAE. Those Psephenids which have no ventral gills, have anal retractile gills and the spiracles are rudimentary (Böving, 1926) or absent. Some DRYOPIDAE, e.g. *Dryops*, have no gills (Böving and Craighead (1931) have figured anal gills in *Dryops auriculatus*). I have examined this species carefully but without finding a trace of anal gills, but most have gills similar to those of *Psephenoides* and in all known genera well-developed spiracles are present.

2. *Internal anatomy.*

The alimentary canal is similar in both families. The central nervous system has the abdominal ganglia much more concentrated in the PSEPHENIDAE than in any known DRYOPIDAE.

Pupae.

In the DRYOPIDAE the pupa is always terrestrial as in some PSEPHENIDAE, e.g. PSEPHENINAE, but it is never concealed under the last larval skin as in the terrestrial PSEPHENIDAE. The dorsal surface of the pupae of the DRYOPIDAE is never modified to resemble the last larval skin, as is the case in many PSEPHENIDAE.

Adults.

1. *External anatomy.*

The antennae of the PSEPHENIDAE are filiform, serrate, pectinate, or ramose, while those of the DRYOPIDAE have the segments beyond the second or third always produced on the inner side to form a close pectinate club. When the antennae are pectinate in the PSEPHENIDAE they are always very long and the ends of the produced segments are widely separated, so that in no case do they have the appearance of a club. The mandibles of the DRYOPIDAE are always large and stout and have a very well-developed prostheca which is frequently heavily sclerotised in parts. The mandibles of the PSEPHENIDAE are small and weak and the prostheca is delicate and entirely membranous. In the EUBRIANACINAE and PSEPHENOIDINAE the postmentum is undivided, whereas in all DRYOPIDAE it is divided. In all DRYOPIDAE the elytra are hard and meet on the middle line of the body, but in the PSEPHENIDAE the elytra are much softer and leathery and are sometimes not contiguous. In the PSEPHENIDAE the coxites of the female genitalia are always symmetrical and each is provided with a movable stylus, whereas in the DRYOPIDAE they are usually asymmetrical and styli are always absent.

2. *Internal anatomy.*

The PSEPHENIDAE have no regenerative crypts projecting on the outer surface of the mid-gut, whereas in the DRYOPIDAE the mid-gut is always densely clothed with prominent regenerative crypts. The six Malpighian tubules of

the PSEPHENIDAE always end freely in the body cavity, but in the DRYOPIDAE the distal ends of all six are embedded at least under the outer muscular coat of the hind gut at a point which is at about the middle of its length. The DRYOPIDAE have always (?) more than one sperm tube to each testis and these sperm tubes are always collectively enclosed in a membranous sheath. In the only male Psephenid available (*Psephenoides*) each testis has only one sperm tube and this is apparently not enclosed in a sheath homologous with that found among the DRYOPIDAE.

The female reproductive system is very similar in both families.

Summary.

The PSEPHENIDAE are not closely related to the DRYOPIDAE. A key to separate the two families follows :—

1. Adults with the antennae filiform, serrate, pectinate, or ramose, but when pectinate never forming a close club. Mandibles small, weak, and with an entirely membranous prostheca. Postmentum divided or undivided. Elytra soft and sometimes not contiguous along middle line of body. Female genitalia symmetrical and each coxite with a movable stylus. Mid-gut without projecting regenerative crypts. Malpighian tubules ending freely in the body cavity. Each testis with a single (?) sperm tube which is not enclosed in an extra sheath. Pupa with the last larval skin attached to its dorsal surface or, if not, with the dorsal surface of the pupa modified to resemble closely the last larval skin. Larvae with a large maxillary articulating area; palp 4-, 3-, or 2-segmented. Abdomen with or without ventral gills, if without then with anal retractile gills. When anal gills are present there are nine pairs of rudimentary spiracles or all spiracles are absent . . . . . PSEPHENIDAE.

–. Adults with the apical segments of the antennae always forming a close pectinate club. Mandibles large, strong, and frequently with part of the prostheca sclerotised. Postmentum always divided. Elytra hard and always contiguous. Female genitalia usually asymmetrical and never with styli. Mid-gut always with prominent regenerative crypts. Malpighian tubules with the distal ends embedded in the walls of the hind gut. Each testis always (?) with more than one sperm tube and these sperm tubes enclosed in a membranous sheath. Pupa not concealed by last larval skin and dorsal surface never modified to resemble the skin of the last instar larva. Larva without or only with an extremely small maxillary articulating area: palp always (?) 4-segmented. Abdomen never with ventral gills; with or without anal retractile gills and always with functional spiracles . . . . . DRYOPIDAE.

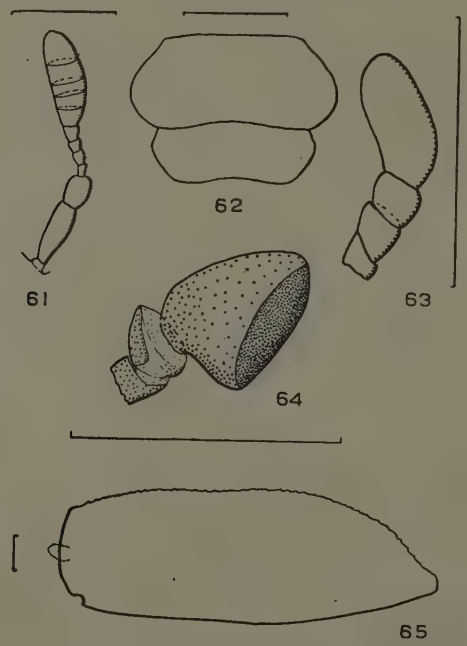
APPENDIX A.

A new genus of Elmini, *Phanoceroides*, is described here. It is important to the new system of classification I have proposed because in every character except that of the pubescence it is nearer the Larini than the Elmini, and it thus affords further proof of the extremely close relationship that exists between these two tribes. A study of the larvae and adults of the new genus leaves one with little doubt that the Larini and *Phanocerus* have, comparatively recently, had a common ancestor.

Phanoceroides gen. n.

Body elongate, subparallel. Clothed on non-tomentose areas with sparse, fine, short setae and also with an occasional long hair; tomentum restricted to the following areas :

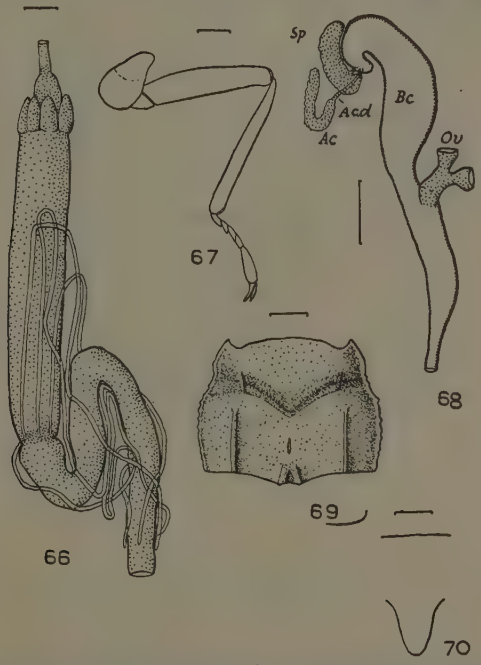
(1) club of antenna; (2) genae; (3) hypomera; (4) epipleura; (5) sides of prosternum, mesosternum, metasternum, and most of abdominal sternites; and (6) most of femora and tibiae. *Head* when seen from below capable of being retracted so that none of the mouth-parts is externally visible. Antenna (fig. 61) 11-segmented and with the five apical segments forming a very compact club. Mandibles with two acute apical teeth; prostheca well developed but entirely membranous. Maxillary palp (fig. 63) 4-segmented and stipes with a well-developed palpifer; galea and lacinia separate and apex of each densely spinose. Labial palp (fig. 64) 3-segmented and prementum with a palpiger. Mentum slightly broader than submentum; submentum posteriorly forming a large depression as is the case in *Phanocerus*; gula similar to that of *Phanocerus*. *Pronotum* (fig. 69) with a longitudinal



FIGS. 61–65.—*Phanoceroides aquaticus* Hntn. (61) Antenna; (62) clypeus and labrum; (63) maxillary palp; (64) labial palp; (65) elytra.

carina on each side on basal half; at anterior two-fifths with a strong transverse impression. *Elytra* striate and punctate; without longitudinal carinae. Hind-wings without a radial cross-vein or an anal cell; with all the branches of the second anal present; and with a complete cross-vein between cubitus and first anal (fig. 71). *Prosternum* (fig. 70) long in front of the anterior coxae; process long and rounded at the tip. Mesosternum with a shallow and posteriorly broadening groove for the reception of the prosternal process. Metasternum with a deep median longitudinal impression which extends to anterior fourth. Sixth ventral abdominal segment (as in all Elmini and *Phanocerus*) not externally visible. *Legs* with the anterior trochantin not externally visible unless the coxae are rotated caudally. Claws (fig. 67) without teeth. *Alimentary canal* (fig. 66) with seven caeca on the anterior margin of the mid-gut. Hind gut with six Malpighian tubules which extend into the

mesothorax and end freely in the body cavity near the rectum. *Central nervous system* with the thoracic and abdominal ganglia as in *Phanocerus*. *Male reproductive system* (fig. 73) with two sperm tubes to each testis which is in the abdomen behind the first segment and partly under the accessory glands; vas deferens (in the single male examined) with the proximal portion not swollen to serve as vesicula seminalis (this varies very much with the degree of sexual development of the animal, and it is possible that at a later and more sexually active stage vesiculae seminales would be developed) and connected proximally to the accessory glands; with two large accessory glands of which the lateral have their mesal margin dorsal to the median and are much larger. Female reproductive system



FIGS. 66–70.—*Phanoceroides aquaticus* Hntn. (66) Alimentary canal; (67) leg; (68) female reproductive system; (69) pronotum; (70) prosternum. (Ac) Accessory gland. (Ac.d.) Duct of accessory gland. (Bc) bursa copulatrix. (Ov) Oviduct. (Sp) Spermatheca.

as figured (fig. 68). My specimen was in a late stage of sexual development and the body was full of eggs so that the number of egg tubes could not be counted, but there appeared to be at least six.

Genotype: Phanoceroides aquaticus sp. n.

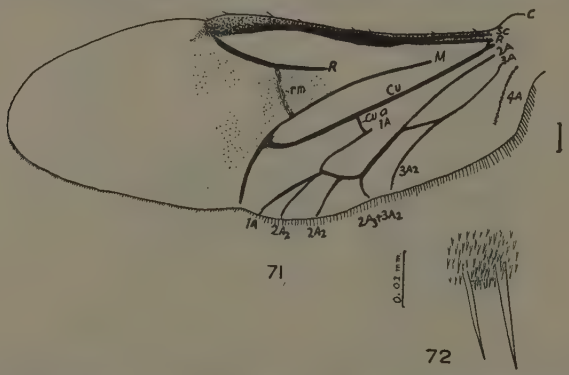
Though belonging to the tribe Elmini, this genus is nearest to *Phanocerus*. Unlike *Phanocerus*, it is truly aquatic, and, as in all the truly aquatic members of both the DRYOPIDAE and ELMIDAE, there are tracts of fine, dense, silky, hydrofuge tomentum on various parts of the cuticle. When these forms are submerged they are not completely surrounded by a film of air.

Phanoceroides is similar to *Phanocerus* in the following characters: (1) size and general shape of the body; (2) structure of the antennae; (3) structure of the mouth-parts and head, particularly that of the posterior concavity of the submentum which in the ELMIDAE occurs only in these two genera; (4) structure of the prosternum; (5) groove of the mesosternum; (6) alimentary canal which differs only in having seven caeca in *Phanoceroides* and eight in *Phanocerus*; (7) the brain and the remainder of the central nervous system has the same external form in both; and (8) the male reproductive system which in both has two sperm tubes to each testis, vas deferens opening proximally to the accessory glands, and the two pairs of accessory glands of which the lateral are the largest and longest.

Contrary to what one would expect from the habits of these two, the wing of *Phanoceroides* is that of a better flier, *i.e.* the venation is more complete.

Phanoceroides aquaticus sp. n. (figs. 61–73).

Male: Length, 3·1 mm.; breadth (across broadest point which is across apical two-fifths of elytra), 1·3 mm. Elongate, subparallel, feebly convex. Dorsal surface with fine,



FIGS. 71–72.—*Phanoceroides aquaticus* Hntn. (71) Wing to show venation (after Forbes); (72) microtrichia on apical inner margin.

testaceous hairs which are partly recumbent and are about 0·02 mm. long and usually separated by from two to four times their lengths; also with similar but erect hairs which are very sparse and about 0·10 mm. long. Ventral surface with tomentum golden and shining. Cuticle reddish-brown, with antennae, mouth-parts, and claws testaceous; for the most part feebly shining and minutely alutaceous. *Head* from base of antenna on each side with a feeble, broad depression extending posteriorly to meet in a curve at top; surface with round punctures which are about 0·02 mm. broad, separated by from two to four diameters. Clypeus and labrum as figured (fig. 62); anterior margin of clypeus and all of labrum with surface shining and punctate, with round punctures about half as coarse as those of head, separated by one to two diameters; apical and lateral margins of labrum densely clothed with fine golden hairs which are about 0·10 mm. long. *Pronotum* as figured (fig. 69); surface punctate like frontal region of head but more sparsely so and at sides with numerous granules which are slightly coarser and denser than discal punctures. *Elytra* (fig. 65) nearly three times as long as pronotum (2·25 mm.: 0·85 mm.), gradually broadening to its broadest point which is at apical two-fifths, humeri only feebly gibbous, apices conjointly and feebly rounded, lateral margins with a feeble and sparse crenation

due to granules similar in size to those of pronotum, intervals flat but with second and third for a short distance at base feebly convex; surface of intervals without distinct punctures; striae with punctures round to quadrate, separated longitudinally by from less than one to one diameter and from one-half to as broad as intervals; towards sides punctures become denser and coarser but towards apex finer and sparser. Sternum of thorax with punctures similar in size to those of sides of elytra, usually round, and confluent to separated by two diameters. Prosternal process at middle with a broad, feebly convex line extending from apex to base. First abdominal segment moderately strongly concave at middle, with lateral carinae

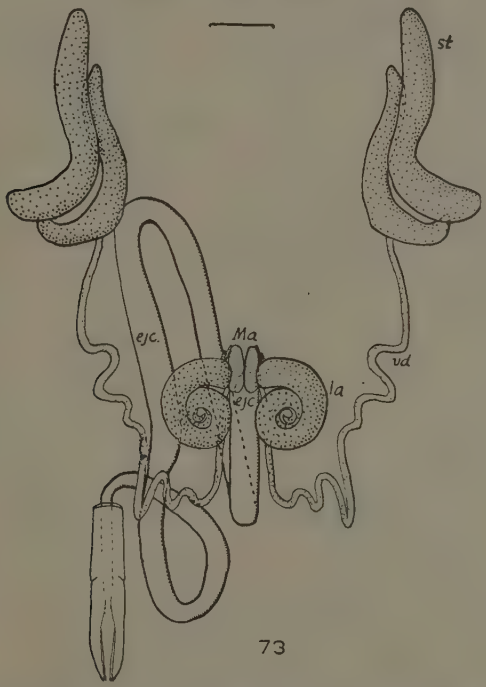


FIG. 73.—Male reproductive system of *Phanoceroides aquaticus* Hntn. (la) Lateral accessory gland. (Ma) Median accessory gland. (ejc) Ejaculatory duct. (st) Sperm tube. (vd) Vas deferens.

extending to its posterior margin; apical margin of fifth sternite with a deep sinuation on each side and with middle rounded. *Genitalia* as figured (fig. 73).

Female: Externally similar to male.

Type: BRAZIL: State of Pará, Manaos, alt. about 200 ft., ♂ ix.1937 (*H. E. Hinton*). Now in the British Museum (Nat. Hist.) collection.

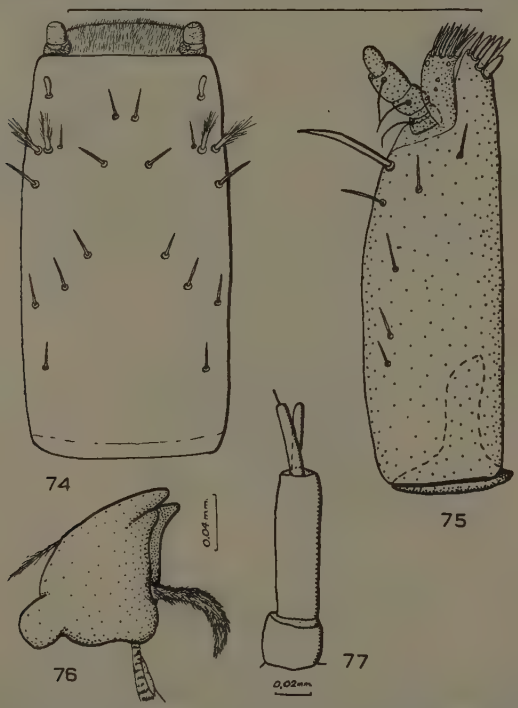
Paratypes: Five with same data as above. Three of these are on glass slides.

Larva.

By elimination and according to locality, the larva of this species has been determined.

Generic characters.

Body flattened, subparallel. *Head* when viewed dorsally exposed and not concealed by the pronotum, with one ocellus on each side. Antenna 3-segmented and not retractile. Fronto-clypeal suture present though not very distinct. Mandibles of both sides similar and with three subacute apical teeth; prostheca long, slender, and densely hairy. Maxillary palp (fig. 75) 4-segmented and stipes showing no differentiation into a palpifer. Labium (fig. 74) with the postmentum undivided; palp 2-segmented and prementum



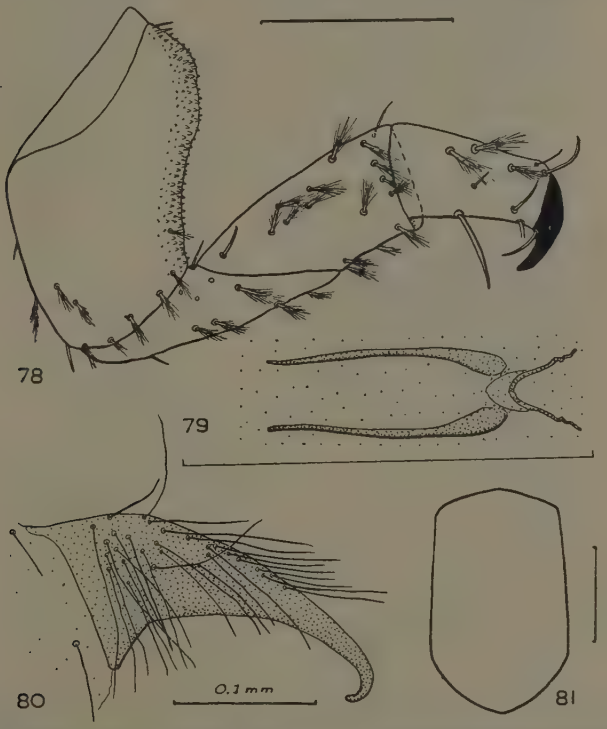
FIGS. 74–77.—*Phanoceroides aquaticus* Hntn. larva. (74) Ventral view of labium; setae of prementum were not counted but are put in to give general appearance; (75) ventral view of right maxilla; (76) dorsal view of left mandible; (77) dorsal view of right antenna.

without a palpiger. Hypopharynx with a heavily sclerotised rod on each side. Ventral sutures well developed. *Prothoracic pleura* undivided and meeting anteriorly on the middle body line. Meso- and metathoracic pleura divided into three parts. Abdominal segments one to eight with pleura bounded by tergo- and sterno-pleural sutures. Operculum with two sclerotised claws attached to its dorsal membrane. *Spiracles* biforous, present on the mesothorax and first eight abdominal segments. Tracheae with well-developed air sacs. Three tufts of retractile anal gills. *Alimentary canal* with a dorsal oesophageal sclerite (fig. 79) and anterior to this with a complete ring of tubercles and spines. Hind gut with six Malpighian tubules which end freely in the body cavity near the rectum. *Central*

nervous system similar to that of *Phanocerus*, with three thoracic and eight abdominal discrete ganglia.

Description of mature larva of *Phanoceroides aquaticus* Hntn. (figs. 74–88).

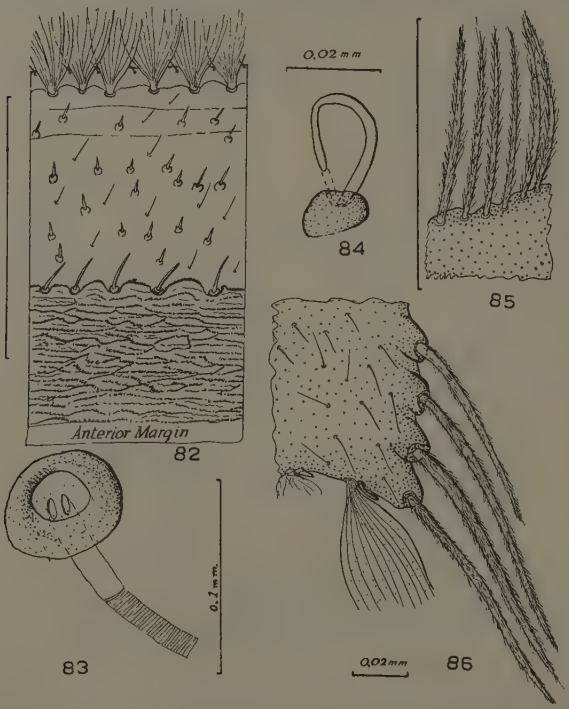
Length, 5·2 mm.; breadth (across broadest point near base of metathorax), 1·7 mm. Cuticle brownish-testaceous to brown. *Head* rectangular but broadest near base where it is broader than long (0·47 mm.: 0·35 mm.); coronal suture straight and 0·12 mm. long; frontal suture extending nearly in a straight line to base of antenna. Cuticle on a broad belt nearly as long as coronal suture with only an occasional puncture, elsewhere with round punctures which are about 0·022 mm. broad and are usually separated by from one



Figs. 78–81.—*Phanoceroides aquaticus* Hntn. (78) Anterior face of right front leg; (79) oesophageal sclerite; (80) dorsal view of right opercular claw; (81) operculum.

to four diameters; from the punctures fine setae arise which are usually slightly longer than their respective punctures; on genae setae are often much longer here being 0·05 mm. to 0·11 mm. long. Antenna (fig. 77) as figured. Clypeus transverse, broader than long (about half as long as second antennal segment), with fronto-clypeal suture scarcely visible. Labrum broader than long (0·15 mm.: 0·11 mm.); anterior margin truncate and angle on each side broadly rounded; epipharynx with tracts of very fine and short setae. Mandibles (fig. 76) of both sides similar, with three apical subacute teeth, and a long, narrow, hairy prostheca, outer lateral side at about middle with a long plumose seta. Maxilla (fig. 75) with setae as figured. Labium (fig. 74) with setae as figured. *Thoracic* and

abdominal terga with proportions as shown in fig. 87. Surface throughout tuberculate (fig. 82); anterior margin of each segment except prothorax with a transverse row of flat tubercles from each of which arises a large seta (fig. 82); on anterior third of meso- and metathorax and on anterior two-fifths of other segments this row is present except on ninth segment where it is present on anterior seventh; anterior to this row of tubercles all segments are finely and transversely rugose; transverse row of tubercles always complete. Lateral margins of all segments with long and plumose setae (fig. 86); posterior margin of all except ninth with flat overlapping setae (fig. 82). *Sternum* sclerotised as figured



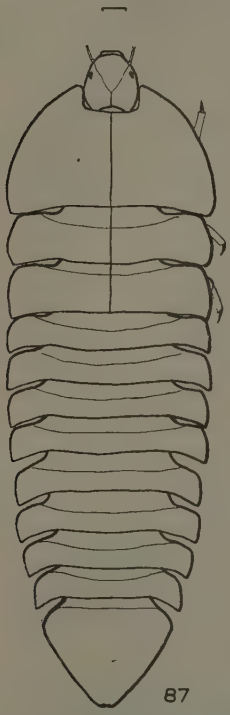
FIGS. 82–86.—*Phanoceroides aquaticus* Hntn. (82) Right side of third abdominal tergite; (83) fifth abdominal spiracle; (84) a seta from the surface of the metasternum; (85) a portion of the row of plumose setae on the anterior margin of the propleurum; (86) lateral margin of third abdominal tergite.

(fig. 88). Abdominal segments three to eight with sterna sclerotised as figured (fig. 88) for second. Ninth with an apical operculum (fig. 81) which carries two sclerotised claws (fig. 80). Anterior margin of propleura with a row of long plumose setae (fig. 85); cuticle of sternites with tubercles usually finer than those of tergites and much sparser, the setae which arise from these sometimes straight and sometimes curled over (fig. 84) so that a complete ring is formed. *Legs* all nearly similar in size, chaetotaxy of front leg (fig. 78). *Spiracles* opening laterally on mesothorax and first eight abdominal segments, biforous, all similar to fifth abdominal spiracle (fig. 83); with cuticle around spiracles elevated to form low but well-developed tubercles.

Immature stages: larvae probably representing three earlier instars have been studied, and they are similar except in size to the mature larvae.

Biology: Found under stones in small to large (2–20 metres) fast-flowing streams of clear water. The gut contents indicate that they are phytosaprophagous.

Specimens examined: Brazil: State of Pará, Manaos, alt. about 200 ft., 32 ex., ix.1937 (*H. E. Hinton*).



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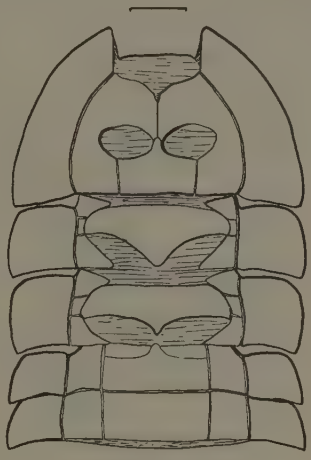

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Figs. 87–88.—*Phanoceroides aquaticus* Hntn. (87) Dorsal view of mature larva; (88) ventral view of mature larva.

Appendix B.

A description of the larva of *Lutrochus* Er.

By elimination and according to locality three species of larvae have been determined to belong to the genus *Lutrochus* Er.

A key to the larvae of *Lutrochus* Er.

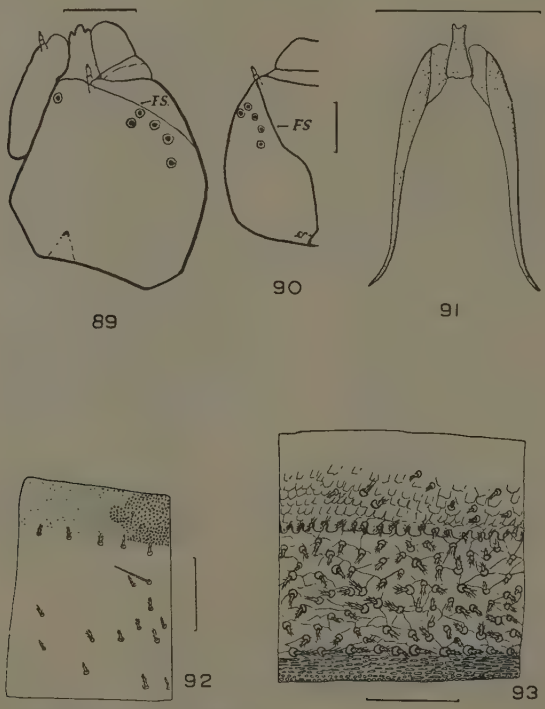
1. Dorsal surface of ninth abdominal segment flat; tergites of mesothorax, metathorax, and first eight abdominal segments with a transverse row of large, dense tubercles on anterior fourth or fifth of each segment. French Guiana . . . . . *L.* sp.?

–. Dorsal surface of ninth abdominal tergite convex; tergites of last two thoracic and first eight abdominal segments without an anterior row of large, dense tubercles . . . . . 2.

2. Tergites of abdominal segments six to nine densely punctate. Bolivia
L. montanus Grouv.

–. Tergites of abdominal segments six to nine densely tuberculate. Cuba
L. geniculatus Chev.

The undetermined species from French Guiana is selected for a detailed description as it is the only species represented in my collection by more than one specimen.

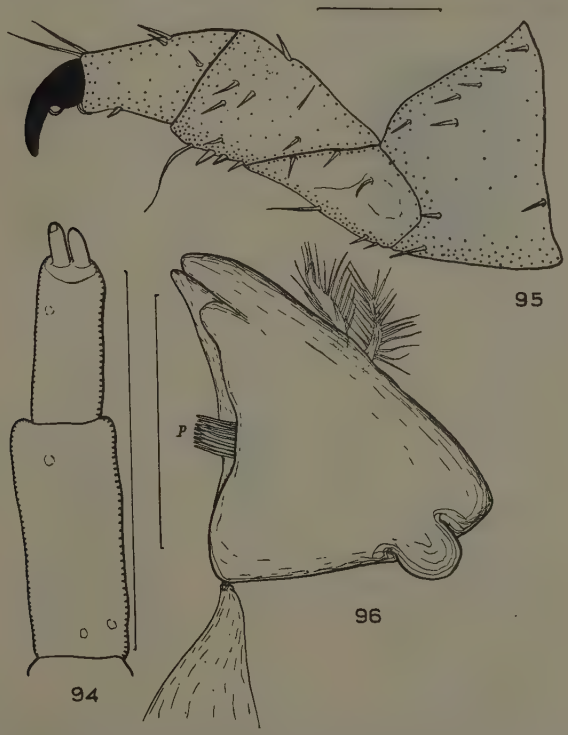


Figs. 89–93.—*Lutrochus* sp. ? (89) left lateral view of head; (90) dorsal view of left half of head; (91) oesophageal sclerite; (92) left half of first abdominal sternite; (93) right side of third abdominal tergite.

Description of mature larva of *Lutrochus* sp. ? (figs. 89–105).

Length, 8·0 mm.; breadth (across broadest point near base of metathorax), 1·32 mm. Body parallel-sided and cylindrical. Cuticle on dorsal side brownish-testaceous to brown, with numerous poorly defined paler spots on head and pronotum, but from mesonotum to eighth abdominal tergite with paler areas forming three broad, irregular, longitudinal stripes on each side of median line; ninth tergite with centre area dark brown and sides from base to posterior sixth paler, the pale area being much broader on posterior half. Cuticle ventrally pale yellow and unicolorous except for operculum which is dark brown and has on each side near middle a well-defined paler spot. *Head* nearly round, slightly broader than long (0·75 mm.: 0·85 mm.); epicranial and frontal sutures as figured (fig. 90).

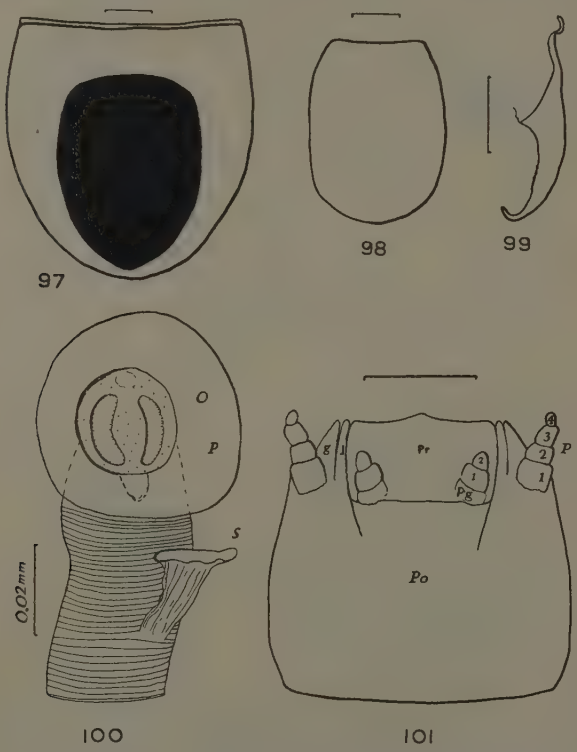
Cuticle sparsely pubescent, with long hairs (about 0·15 mm. long), throughout finely, densely alutaceous; most of surface with round punctures, generally about 0·02 mm. broad, confluent to separated by two diameters; posteriorly these punctures become finer and sparser and on each side near labium are replaced by low tubercles which are equal in size and density to the replaced punctures. Ocelli with six large and distinct facets on each side distributed as figured (fig. 89). Antennae (fig. 94) 3-segmented and capable of being retracted into head up to middle of the second segment. Clypeus short, with anterior margin truncate and angle on each side broadly rounded. Labrum as long as basal segment of antenna, with anterior margin feebly and broadly emarginate and angle on each



FIGS. 94–96.—*Lutrochus* sp. ? (94) Dorsal view of left antenna; (95) anterior view of right front leg; (96) dorsal view of right mandible.

side broadly rounded; basally with a complete transverse row of dense, golden hairs which are about 0·018 mm. long and near apex with a similar row of much shorter hairs; epipharynx with tracts of dense, fine setae. Mandibles (fig. 96) of both sides similar, with three apical teeth, with an unusually short prostheca (p) consisting of a number of close, erect setae, outer lateral side with two large multi-branched setae. Maxilla (fig. 101) with palp 4-segmented and stipes showing no differentiation of a palpifer; galea and lacinia separated and apex of each densely spinose; stipes completely fused with the postmentum, no evident suture between them and the ventrally folded portion which represents the cardo (the apical part of this ventrally folded portion has inserted on it the characteristic fan-shaped group of fibres—the promotors of the cardo—which arise on the postgenae).

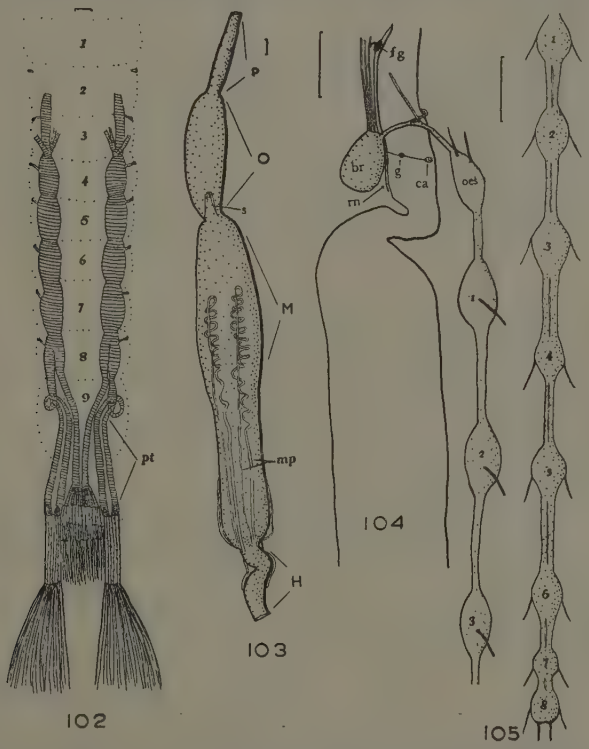
Labium (fig. 101) with postmentum undivided and submento-mental muscles absent; labial palp 2-segmented; prementum with a well-marked palpiger. *Pronotum* longer than broad (1·42 mm. : 1·25 mm.), sides subparallel, slightly broader at base than apex. Cuticle sculptured as frontal region of head but also transversely and sparsely rugose; basal and anterior margins with belts about 0·12 mm. long which are finely and densely alutaceous with minute flat tubercles (similar to those of anterior margin of third abdominal tergite, fig. 93); in front of posterior belt with a single row of moderately densely set, convex tubercles which are about as large as punctures; posteriorly and at



Figs. 97–101.—*Lutrochus* sp.? (97) Ventral view of ninth abdominal segment; (98) operculum; (99) ventral or inner view of opercular claw; (100) mesothoracic spiracle; (101) ventral view of first and second maxillae.

sides with an occasional tubercle similar in size and shape to those of posterior row; from all tubercles and punctures setae arise which are scarcely longer than the diameters of their respective tubercles or punctures; lateral margins of terga have a fringe of moderately dense setae which are generally from 0·12 mm. to 0·25 mm. long; elsewhere on tergum with an occasional long seta. *Mesonotum* broader than long (1·30 mm. : 0·75 mm.), similar to pronotum except that here most of punctures are replaced by tubercles and before anterior alutaceous belt is a complete transverse row of dense

tubercles which are flat on top and slightly larger than any others on the segment. *Metanotum* and tergites of first eight abdominal segments similar in sculpture and general proportions to mesonotum but abdominal tergites have not the definite lateral setal fringe of thoracic ones, lateral setae of abdominal tergites being much more scattered; tubercles of abdominal tergites become sparser on posterior segments. Sculpture on each side of median line is figured for third abdominal tergite (fig. 93). Ninth tergite flat with proportions as figured (fig. 97) and only anterior row of dense tubercles; lateral setae arranged



FIGS. 102–105.—*Lutrochus* sp.? (102) Dorsal view of abdominal tracheae and tracheal gills showing connections; (103) alimentary canal; (104) lateral view of central and stomodeal nervous systems; (105) dorsal view of thoracic and abdominal ganglia. (br) Brain. (ca) Corpora allata. (fg) Frontal ganglion. (g) Occipital ganglion. (H) Hind gut. (M) Mid-gut. (mp) Malpighian tubules. (O) Oesophagus. (oes) Sub-oesophageal ganglion. (rn) Recurrent nerve.

in two rows which converge near apex to form one row. *Sternum* of thoracic segments mostly membranous, but with narrow pleura moderately heavily sclerotised. Pleura of first two abdominal segments bounded by sutures; pleura of third segment without a tergo-pleural suture but with a distinct sterno-pleural suture; segments four to eight and basal part of ninth forming complete sclerotised rings. Sternal region of first eight abdominal segments sculptured similarly to that of first segment (fig. 92). Posterior sternal region of ninth forms operculum as figured (fig. 98); attached to operculum on inner side are two claws (figs. 57 and 99) which are devoid of setae. *Legs* all somewhat similar to front leg

(fig. 95), increasing in size posteriorly. *Spiracles* opening on sides of mesothorax and first eight abdominal segments on about anterior fifth of each segment; all spiracles biforous and similar to mesothoracic spiracles (fig. 100). Principal tracheae of abdomen and three tufts of retractile tracheal gills as figured (fig. 102). When normally retracted into body, the two tufts of ventro-lateral gills extend to anterior margin of seventh segment and dorso-mesal tuft to anterior margin of ninth segment; when in body apical branches of tracheae which supply gills (pt) are folded back along main tracheal trunks. *Alimentary canal* (fig. 103). On dorsal posterior margin of oesophagus is a sclerotised structure (fig. 91) embedded in wall of gut. Six Malpighian tubules (mp), all of which run forwards to about apical fourth of mid-gut and, when returning, are frequently and narrowly sinuate; distal ends of these tubes are closely applied to walls of rectum *Central nervous system* and stomodeal nervous system as figured (figs. 104 and 105).

Specimens examined: French Guiana: St. Laurent du Maroni, 42 ex., x.1937 (*H. E. Hinton*). All were taken on submerged stones, sticks, and logs in small and rapidly flowing streams.

The smallest larva in the collection is 5·0 mm. long, but it agrees in all essentials with the description given of the mature larva.

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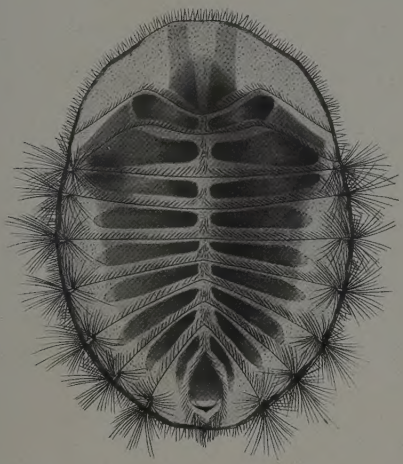
Explanation of Plate 1.

Figs. 1–4.—*Psephenoides* sp.? (1) Dorsal view of pupa; (2) ventral view of pupa; (3) dorsal view of larva; (4) ventral view of larva.



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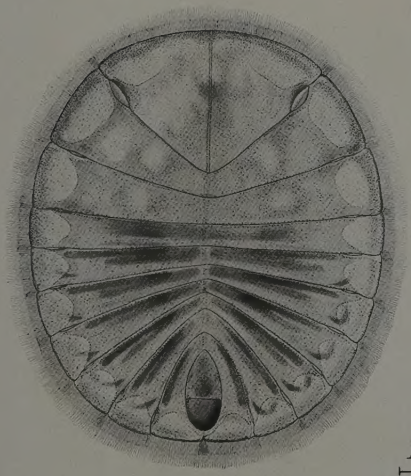

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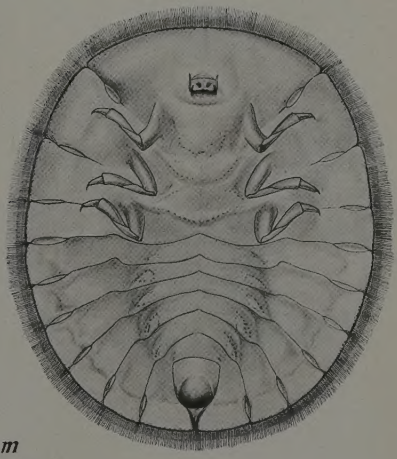

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Larva and pupa of *Psephenoides* sp.